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UNITED STATES DEPARTMENT OF AGRICULTURE
BULLETIN No. 903

Contribution from the Bureau of Entomology
L. O. HOWARD, Chief

Washington, D. C. PROFESSIONAL PAPER April 22, 1921

THE GRAPE PHYLLOXERA IN CALIFORNIA

By

W. M. DAVIDSON, Scientific Assistant, and
R. L. NOUGARET, Entomological Assistant,
Deciduous Fruit Insect Investigations

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By W. M. DAVIDSON, *Scientific Assistant*, and R. L. NOUGARET,[2] *Entomological Assistant, Deciduous Fruit Insect Investigations.*

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CALIFORNIA HISTORY.

EARLY VINE PLANTING IN CALIFORNIA.

The grape phylloxera is not native to California. It has long been recognized as originating in North America, but its native habitat is east of the Rocky Mountains. The insect has not established itself upon the native vine of California (*Vitis californica*) in the wild state, whereas in Arizona it is established on native vines.

[1] *Phylloxera vitifoliae* (Fitch).

[2] Now in charge, Viticulture Service, California Department of Agriculture, Sacramento, Calif.

NOTE.—In connection with other work in California, the office of Deciduous Fruit Insect Investigations, Bureau of Entomology, in cooperation with the Bureau of Plant Industry, has been engaged in an investigation of the grape phylloxera during several years past, with principal headquarters for the work at Walnut Creek. The work inaugurated by E. L. Jenne, upon his death was taken over by S. W. Foster, assisted by R. L. Nougaret. Upon Mr. Foster's leaving the service, the investigation was continued by Messrs. Nougaret and Davidson, the latter giving especial attention to biological and life-history studies and the former to investigations in the field and to remedial operations. The present report deals with the history, injuries, and life history of the insect in California. Remedial measures will be made the subject of another publication. It has been necessary to omit an extended bibliography of the subject.—A. L. QUAINTANCE, *Entomologist in Charge of Deciduous Fruit Insect Investigations.*

More specifically, the insect is a native of the Mississippi Valley, where the vines have developed a resistance to phylloxera, and such species as *Vitis riparia*, *V. rupestris*, *V. aestivalis*, etc., thrive, notwithstanding the presence of the insect. These wild species possess varying degrees of immunity and through scientific selection and hybridization have yielded types of vines possessing inherent degrees of immunity, known to viticulture as resistant vines, or resistant stocks when designated as a root upon which to graft commercial varieties of grapes in order to circumvent the ravages of phylloxera.

Vitis californica is a wild species of vine found not only in California but throughout the Pacific coast. Because normally found free of phylloxera in its wild state, it was at one time tried out as a resistant stock upon which to graft commercial varieties, but proved a complete failure in all but one or two instances. Even under normal conditions and environment, when once attacked it succumbs to the injury by the insect.[3]

The Mission grape is a cultivated variety of *Vitis vinifera*, and although of European origin, its introduction to the Pacific coast is so intimately related with the first settlement of California under Spanish rule that it well deserves the oft-attributed title of "California grape" (7)[4]. The Mission grape was introduced into California by the Padres of the Roman Catholic missions. As early as 1524 (18, p. 17), while Cortez was governor of Mexico, then called New Spain, seeds and plants were most often part of the cargo of vessels plying between the mother country and her colonies. Grapes and olives are plants mentioned as being among these. It is to be assumed that about that time *Vitis vinifera* varieties were introduced into Mexico from Spain[5] through both cuttings and seeds (1, v. 2, p. 131–133; v. 3, p. 613).

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[3] In the Annual Report of the California Board of State Viticultural Commissioners for 1887, published in 1888, pages 47–48, may be found the following: "While visiting Mr. Hagan's vineyard, we were led to examine an old vine—*V. californica*—which appeared like one infested with phylloxera. This surmise proved correct * * *.

"The commission has often sought for evidences of phylloxera on our wild vines in their native state, but up to this time none has been found, this being the first case of the kind discovered." (See "Literature cited (5)," p. 127.)

[4] Numbers in parentheses refer to "Literature cited," p. 127.

[5] In this connection F. T. Bioletti, professor of viticulture at the University of California, writes as follows: "No one has yet been able to trace the Mission grape with certainty to any European variety. It is a remarkable coincidence, if nothing else, that a Sardinian grape known as the Monica resembles the Mission very closely. The Monica is said to be a favorite grape of the monks in Sardinia, and it seems probable that the missionary monks of Mexico, finding it difficult to transport cuttings from their original homes, obtained seeds of the grape which they liked the best and that from the seedlings grown they chose the one which most resembled the grape they were looking for. If this is in accordance with the facts, the Mission is simply a seedling of the Monica."

He further advances the suggestion that the Mission might be a seedling of the Monica, as published in a report (2) of the viticultural work of the agricultural experiment station of the University of California * * * 1887–1893.

Later, in the early part of the eighteenth century, a long line of missions was established throughout the peninsula of Lower California, the Mission of Loreto being the first, in 1697. These missions all grew grapes. The vines were furnished to them originally by the colonies of Mexico. As missions were founded, products and plants were furnished to the new one by the older established ones, and grapes are almost always mentioned as being cultivated by the Padres.

The Mission of San Diego was the first to be founded in upper California, and the vines planted there were brought from the missions of Lower California. As no other variety but the Mission grape is known to have been cultivated by the different missions which were founded in after years, it is to be presumed that it was introduced into this State with the founding of the Mission of San Diego, 1769.

The Mission is a long-lived, vigorous, and thrifty vine, as is attested by two remarkable specimens. The one planted in 1775, and still living, is on the property of the San Gabriel Mission in Los Angeles County, is trained on an arbor, covers 9,000 square feet, and its trunk just below the surface of the soil has a circumference of 9 feet. The other, planted in 1842 near Carpenteria, died in 1915, presumably of the "Anaheim disease." It measured at its base 8½ feet in circumference; at a height of 6½ feet it divided into three branches, one of which measured 3½ feet in circumference. As an arbor it covered one-fourth acre, and in 1895 yielded its maximum crop of 10 tons, its average crop being estimated at 5 tons.[6]

The Mission grape in early days was planted by the Padres around the missions and was used both as a table grape and especially for making wine. Gen. Vallejo (7) is authority for the statement that the Mission grapes grown at the Sonoma Mission were of a better quality than those grown at the other missions in California, and that a recognized superior quality of wine was made from them.

It was probably because of this reputation that the first commercial vineyards of wine grapes were established in the vicinity of the town of Sonoma. In this district the grape phylloxera was first discovered, and the dying of the vines, which for some time had puzzled the viticulturists, was finally determined to be the result of this insect's attack. An importation of vines from Europe of unparallelled importance up to that time for California, and one which may adequately be termed a "pioneer importation," occurred at about this time and very shortly prior to the discovery in France of the phylloxera, thereby furnishing grounds for the subsequent report, more or less widely spread throughout the State and which persists

[6] Details of its history can be obtained from the secretary of the Carpenteria Chamber of Commerce.

even at this late date, though refuted at different times by investigators, that this importation of European vines was responsible for the introduction of phylloxera into California. This is a mistaken idea. The history of the grape industry virtually proves that the insect was imported with American species or varieties of grapes from east of the Rocky Mountains.

FIRST DISCOVERY OF GRAPE PHYLLOXERA IN CALIFORNIA.

The first evidence of phylloxera infestation in California dates as far back as 1858. The dissemination of phylloxera continued for years in California before the existence of the pest was known, although its destructive work was observed, commented on, and designated a disease of vines from unknown causes. Reference to the first discovery and determination of the insect in California is to be found in a report (4, p. 108–111) dated August 28, 1880, and submitted by H. Appleton. In his report the first ravages witnessed in California are discussed, and from them is inferred the date of introduction of the insect. Extracts from this report follow:

> On the nineteenth of August, 1873, an insect was found on the roots of grapevines by H. Appleton and O. W. Craig, in the vineyard of the latter, situated two miles north from Sonoma Town, on the west side of Sonoma Creek. An investigation was ordered at the time, for though the insect was identified as "the insect, or louse, known in Europe by the title of phylloxera-vastatrix, and in the United States as pemphygus vitifoliae," there existed a doubt in the minds of the investigators, because the injury was confined wholly to the roots of the vine, and no symptoms of injury such as recorded in Europe and in Eastern North America could be detected on the leaves.
>
> From information received from Mr. A. F. Haraszthy and Captain E. Cutter, Superintendent of the Buena Vista Company's vineyards, I am able to give the following facts in regard to their large vineyards:
>
> A vineyard of about one thousand vines was planted in 1834–35, and was watered every year. In 1850 and 1852 the vineyard was largely increased, and the system of irrigation was stopped. In 1857 about two hundred thousand vines were set out, and in 1858 one hundred acres were put in vines (six hundred and eighty vines to the acre). Again, in 1860, fifty acres were laid out. In 1862, Colonel A. Haraszthy planted 70,000 European vines, and it was among these vines the disease increased most rapidly.
>
> In the Spring of 1863 the Buena Vista Company was incorporated, and in the Spring of 1864 that company planted 100,000 vines.
>
> As early as 1860 decayed and dying vines were noticed in the vineyard, and they were taken up and others planted in their places. An examination was made to discover the cause of the disease in these vines, and it was attributed to alkali water, which was found a few feet underground. The roots were decayed. No examination by microscope of these roots was made. Vines died from time to time, showing short growth, small and colorless grapes, early yellow leaves—in fact, all the symptoms were observed of vines dying from the vine pest.
>
> In 1868 about 3 acres of diseased vines were taken up (planted in 1850) on the north side of the dwelling house, and new vines planted, which grew well, showing little signs of decay till they were four years old, at which time (1873) the Phylloxera Committee, of the Viticultural Club, found the phylloxera on several vines.

The facts of this statement are significant and by no means ambiguous if considered in the light of the knowledge possessed to-day of the life history and habits of phylloxera, the nature of its injury, and the progress of its ravages.

This report also indicates how and when the first impulse was given to the development of the grape and wine industries of the State, then in their infancy. As interest grew in this direction, better varieties of grapes than the Mission would naturally be sought and given a trial. This was the case with the eastern variety of grape, the Catawba, a vine susceptible to the attack of phylloxera because of its fleshy roots and successfully grown at that time in the East as a wine grape. A weekly agricultural paper, the California Farmer (6), under date of Thursday, January 23, 1855, in an editorial article entitled "The Catawba Grape," says:

> We sincerely esteem the Catawba grape, one of the very best varieties for cultivation in California. Longworth of Ohio, whose famous Catawba Champagne is now esteemed equal to any wine imported, says it is the very finest wine grape known. Will be found far superior to our California Grape [Mission]. We earnestly urge our cultivators to give the Catawba a careful trial.

The same agricultural periodical from time to time that same year published other articles[7] eulogizing not only the Catawba but also other vines of eastern varieties and quoting fabulous yields in wine and profits.

Articles such as these undoubtedly influenced the planting of eastern varieties, if only as an experiment. Can it be doubted that many vines were brought from the East to California and the phylloxera introduced with them?

The variety of grape planted in 1850–1852 in the Buena Vista vineyard is not mentioned. It is more than likely that the major part of the planting was of Mission. If these vines were inoculated with phylloxera shortly afterwards by means of a few eastern grapevines planted near by, the vineyard would have experienced a spread of invasion as related above by Appleton. Evidence of the insects' injury would be apparent as affecting only a few vines during a few years or up to about 1860, and eight years later the vines, covering an area of 3 acres, would have become so dwarfed and nonproductive, with perhaps a few dead, that it would be necessary to grub them up. That this vineyard trouble was due to phylloxera is emphasized by the further statement that the 3 acres were again replanted with new vines, and during the four following years (1869–1872) the vines were again affected in a similar manner, but to a slighter degree, just as a recurrence of infestation would act if vines were planted in infested soil. Finally, in 1873, just five years

[7] E. g., "What are the best grapes;" "Extracts of the Cincinnati Gazette."

after the replanting of the 3 acres, the committee of the Viticultural Club discovered the phylloxera on the roots of several of the replants.

The history of this vineyard proves conclusively by direct and circumstantial evidence that the trouble was due to phylloxera. It localizes the infestation, describes the progress and spread of the injury, and, by fixing dates, determines the period of time the progress covered. Finally, the presence of the insect is discovered and its identity determined.

In 1861 Gov. Downey, of California, appointed three commissioners to work in the interests of the grape industry, two of the members of this commission being Don Juan Warner and A. Haraszthy. The latter was sent to Europe to purchase for the State for distribution different varieties of grapes, and the result was the importation of 200,000 cuttings and rooted vines, comprising 1,400 different varieties of grapes from all the vine-growing countries of Europe and also from Asia Minor. It may be that some of these imported rooted vines harbored phylloxera, which already had caused considerable damage to vines in France, although the insect was only discovered in that country the following year (1862). It is quite likely that a good portion of the 70,000 vines planted out on the Buena Vista vineyard in 1862 and referred to in Appleton's report were propagated from this importation and that the pest may have been introduced simultaneously with the planting of the vines. The rapid destruction of the vineyard, as stated, however, could have been brought about in the case of the young vines just as well by infestation communicated by the old vineyard.

The history of the Orleans Hill vineyard furnishes an insight into the methods of establishing vineyards with varieties of grapes imported from Europe in the early days of grape culture in California, and helps to give grounds for the belief that the earliest and original introduction of phylloxera into this State was due to eastern varieties of grapes only.

Data of this history are contained in a report, dated 1880, submitted by the owner of the vineyard (4, p. 112). In 1853 the owner imported from Nassau, on the Rhine, in Germany, 15 varieties of grape cuttings (vinifera) and planted them in his garden near Sutters Fort, Sacramento, where they flourished splendidly and showed no signs of disease. In 1859–60 many vines were propagated here for planting the Orleans Hill vineyard in Cache Creek Canyon, Solano County. This vineyard was set out in two different situations, part being on a hillside and part in a flat. In the latter situation the soil was of a stiff clayey nature and the vines did not do as well as on the more friable hillside soil, and this necessitated replanting, for which there were procured later from Napa some Zinfandel vines.

The date when these replants were procured is not specified, but was probably about 1864 or 1865. Before the date of replanting the phylloxera had infested the Sonoma Creek district and had spread to Napa County.

In 1859 a horticultural exhibit was held in the agricultural hall just completed that year at Sacramento, and the records of the State Agricultural Society mention exceptionally good exhibits of grapes by progressive fruit growers. The eastern grape Catawba is twice mentioned.

From another report (4, p. 29–30) we learn to what extent the eastern varieties of grapes were grown prior to 1875 in El Dorado County. No mention is made of earlier dates, but it is more than probable that the European grapes were already supplanting the eastern ones, judging by the few of the latter type which were planted in later years and which to-day are found only in family vineyards and gardens. This report, written by Mr. G. G. Blanchard, commissioner of the State board of viticulture, further stated that what was true of El Dorado County could also be said of Nevada, Placer, Amador, Calaveras, Tuolumne, and Mariposa Counties. A passage reads:

> The proportions and kinds (grapes) growing, taking one hundred as the sum, are as follows: Mission, or native grapes, sixty-eight; Catawba and Isabella, ten; White Muscat, Muscatella, Malaga, six; Tokay, Black Morocco, Malvoisies, one; Zinfandel, Riesling, two. The other thirteen are made up of numerous other varieties, such as Sweet Water, Black July, Hartford Prolific, Cloantha, and Concord, and some others.

In this enumeration eastern grapes would represent approximately 23 per cent of the varieties grown. We thus see the important part played by eastern varieties of grapes in the earliest plantings and can conceive how the pest was introduced directly from its natural habitat.

ACCIDENTAL AND NATURAL SPREAD.

Centers of infestation, when compared according to the modes of dissemination which they engender, are of two kinds: Accidental and natural. An accidental distribution center would be a nursery which imported, unwittingly, phylloxera-infested grapes, propagated the vines, and by so doing bred the insect and disseminated it with the sale and shipment of these vines. The same is true when vines are procured from phylloxera-infested districts. For new plantings or replants, such a center would be the infested locality in Napa, from which the Zinfandel vines were the means of introducing the pest into a locality as yet free from it. In turn, the Orleans Hill vineyard became a natural distributing center because the insect by its natural increase and habit spread to other parts of the same vineyard or even to other vineyards of the district.

Infestation from accidental distributing centers may be avoided by strictly enforced quarantine measures.

Accidental spread has been the main cause of most of the phylloxera infestation throughout the vineyards of California because of its being an initial inoculation, developing later into a center of natural dissemination.

A general survey of the growth of the grape industry, which at times, as in the late eighties and early nineties, attained the proportion of a boom, furnishes an indication of the accidental spread which took place concurrently.

Cuttings were used almost exclusively for planting vineyards in preference to rooted vines, the latter being used for replanting "misses," and even then not commonly used. As will be shown later, there is little, if any, danger in disseminating the phylloxera from cuttings, unless these are heeled in in infested soil while awaiting shipment. It is for this reason that the accidental diffusion was greatly restricted. If rooted vines had been commonly used, originating from the same district as the cuttings, the accidental diffusion would have been so general as perhaps to have precluded before long the growing of vinifera vines on their own roots.

THE WINGED MIGRANT NOT A FACTOR IN SPREAD UNDER CALIFORNIA CONDITIONS.

Profiting by the investigations and experiments that were being carried on in France, the University of California in conjunction with the State Board of Viticulture made extensive efforts to arrest the ravages of the phylloxera, and made investigations pertaining to its life history and habits. These deserve special mention in this report.

Dr. F. W. Morse (16) of Oakland, Calif., during the period 1881–1886, as an assistant in the General Agricultural Laboratory, discovered in the course of his investigations on August 26, 1884, specimens of the gall louse or leaf-inhabiting form of the phylloxera. As is noted under the heading "The gallicole and its relation to California conditions" (p. 95), this is the only recorded instance of the finding in California of the leaf galls. In this connection it may be said that in the experimental vineyards of the Bureau of Plant Industry, United States Department of Agriculture, in which are collected many varieties and hybrids of species of American vines, not a few of which are susceptible to leaf galls when cultivated in the Eastern or Middle States, an exceptionally good field for observation is offered. Mr. G. C. Husmann, under whose direction these vineyards are conducted, states that the leaf gall, to his knowledge, has never been found in them. Extensive correspondence

with entomologists and prominent viticulturists in California elicited the same information.

Laboratory experiments, conducted under favorable conditions to obtain winter eggs with the existing strain of phylloxera in California, have failed to go beyond the production of the winged form in specially devised cages, although in other laboratory experiments the sexed forms were produced and the discovery in the natural state of a single winter egg must be mentioned.

A study of the life history has corroborated the observations of Dr. Morse relating to the sterility of a portion of the winged migrants and to the sterility of some and the debility of the remainder of their progeny. The writers' observations demonstrate that the normal life cycle of the insect in California is wholly parthenogenetic and that the natural spread, or diffusion, is due entirely to young radicicole larvæ possessing migratory instincts, at least during July, August, and September, and to which has been given the name of "wanderers" to distinguish them from "migrants," a term which commonly is applied to winged forms of the Aphididae.

The conclusions of the investigations of Dr. Morse point to the possibility of such a condition, though not affirming that the winged migrant is not responsible for the diffusion of the species in California. The late Prof. E. W. Hilgard (14) shared this view, which he expounded in his report, in which he indicates the discovery by him of one of the first phylloxera spots in Napa Valley, as follows:

> The first phylloxerated "spot" within the Napa Valley was observed by me in 1877, close to the stage road and public highway leading directly from the worst-infested portion of Sonoma, and on which vineyard material was, and is, constantly being hauled back and forth. It is plainly from this highway and its infested wagonloads that the insect has spread in the Napa Valley.

The "spot" alluded to is believed by the writers to have been either in the old Squibb vineyard (10 acres), in the old McClure vineyard adjoining, or in the Callan vineyard (50 acres). All these were located close together. They have long since been pulled up, the land is now pasture, and only a very few of the old original vines still exist, although browsed down by the stock. These vines date back to 1866.

From present knowledge of the biology of the phylloxera, it is believed by the writers that the vineyard material referred to by Prof. Hilgard was responsible for the spread of the pest to this location, but the inoculation was due to the wandering young radicicole larvæ rather than to the winged form.

PHYLLOXERA SPREAD BY PICKING BOXES.

"Vineyard material" may imply many sources of infestation. Besides rooted vines, grape-picking boxes are very likely to trans-

port the insect from one district to another. At times grapes are delivered to the wineries in greater quantities than can be handled, and boxes of grapes are unloaded and left at the winery instead of their contents being emptied into the elevators and the empty boxes returned to the same wagon. Boxes are exchanged, and some from infested districts find their way to uninfested vineyards. Wandering larvæ (wanderers) easily shelter themselves in cracks and joints of boxes while these remain strewn throughout the vineyard waiting to be filled with grapes, and when the boxes are transferred to other vineyards, after having been emptied at the winery, the insects may be released by the shock of the empty box against the ground in the process of unloading.

In their practical experience, certain grape growers have noticed that the first signs of phylloxera in their vineyards appear at places where they have been in the habit of dumping boxes for the convenience of grape pickers.

There were a number of wineries, reputed for the excellence of their wines, in the early-infested district around Glen Ellen, Sonoma, and Los Guillicos, and grapes were hauled to them from afar at about the time vines were dying rapidly in their vicinity. This accounts, no doubt, for the several early centers of infestation which appeared in a short period of time in Napa County.

The pest spread into Napa County from Sonoma County not only along the highway to and beyond the vineyards cited in Prof. Hilgard's report, but also over the ranges of hills referred to in the same report by means of a mountain road which ran over the divide from Sonoma and descended into a long narrow valley (Brown Valley), which itself opened out into Napa Valley quite close to the city of Napa. At the head of Brown Valley and almost on the county boundary line is the Dell vineyard. From the owner, Mr. C. Dell, the following information was obtained: In 1867, 20 acres of Mission grapes were planted with cuttings obtained from the Wing vineyard (then owned by Buhman Bros.), material for which formerly had been secured from the Buena Vista district at Sonoma. After seven years the Dell vineyard began to show signs of phylloxera in small patches, but bore good crops for four years. The Wing vineyard, located close by, began to die at the same time.

The phylloxera was introduced in this case probably by means of picking boxes, or else by rooted vines planted to fill out places where the cuttings had failed. If the dates are correct, the infestation would have been noticed, without the cause being known, in 1874, or about the time it was discovered along the Sonoma highway.

The above data are recorded to indicate how important a rôle this Sonoma Creek district played in the first introduction of the insect into California and how the spread occurred through different chan-

nels. For this reason the early plantings give an idea of how the insect could have been spread before its presence was suspected.

PRACTICAL METHODS EMPLOYED TO ARREST THE SPREAD OF THE PEST.

When the discovery of phylloxera in California was first made known, the grape growers were already acquainted more or less with the havoc it had produced in the vineyards of France, and a panic spread throughout the different grape districts. It soon subsided, however, when the vineyards were not being rapidly destroyed, and even precautionary measures were overlooked.

Of all the grape-growing counties, that portion of Alameda County known as the Livermore Valley district evolved the best organized system of quarantine measures, the aim of which was not to prohibit the importation of vines into the county, but to have cuttings, as well as rooted vines, thoroughly disinfected before they were permitted to be planted.[8]

The disinfectant used was a commercial soluble phenol. Vines were immersed for one-half hour in a solution of 1 part phenol to 60 parts water. Notwithstanding these precautions, vines were introduced without the knowledge of the quarantine commission, and there occurred three distinct centers of infestation from which the pest was remarked to spread with the prevailing summer winds. Two of these centers were planted originally with material from San Jose, and the third with vines from St. Helena, in Napa County.

DISTRIBUTION OF PHYLLOXERA IN CALIFORNIA.

As far as has been observed, Stanislaus, Merced, Kings, and Madera Counties, north of Tehachapi Pass, are free from phylloxera. South of Tehachapi Pass it has not been found so far. Most of the counties named have either enacted ordinances establishing prohibitive quarantine against the importation of grapevines or protective measures subjecting vines to strict inspection and fumigation.

The absence of infestation is without doubt not wholly due to quarantine measures, which were enacted years after the pest had many opportunities to be introduced, but more likely is due to the combined conditions of climate and soil in these counties.

The writers have made a personal investigation of the present status of phylloxera infestation, and have tried to ascertain and estimate approximately the damage caused to the viticultural interests. At this late date, however, there is much difficulty in obtaining information on which to base the estimate. Quite a number of vineyards have been replanted, some as many as three times; property has changed hands, and the history of vineyards has been forgotten. Again,

[8] Data personally contributed by Charles A. Wetmore, formerly chief executive of the State board of viticultural commissioners.

no traces exist of large vineyards pulled up but not replanted, and thus accurate data are unobtainable. Therefore a summarized statement based upon data to be found in the various reports of

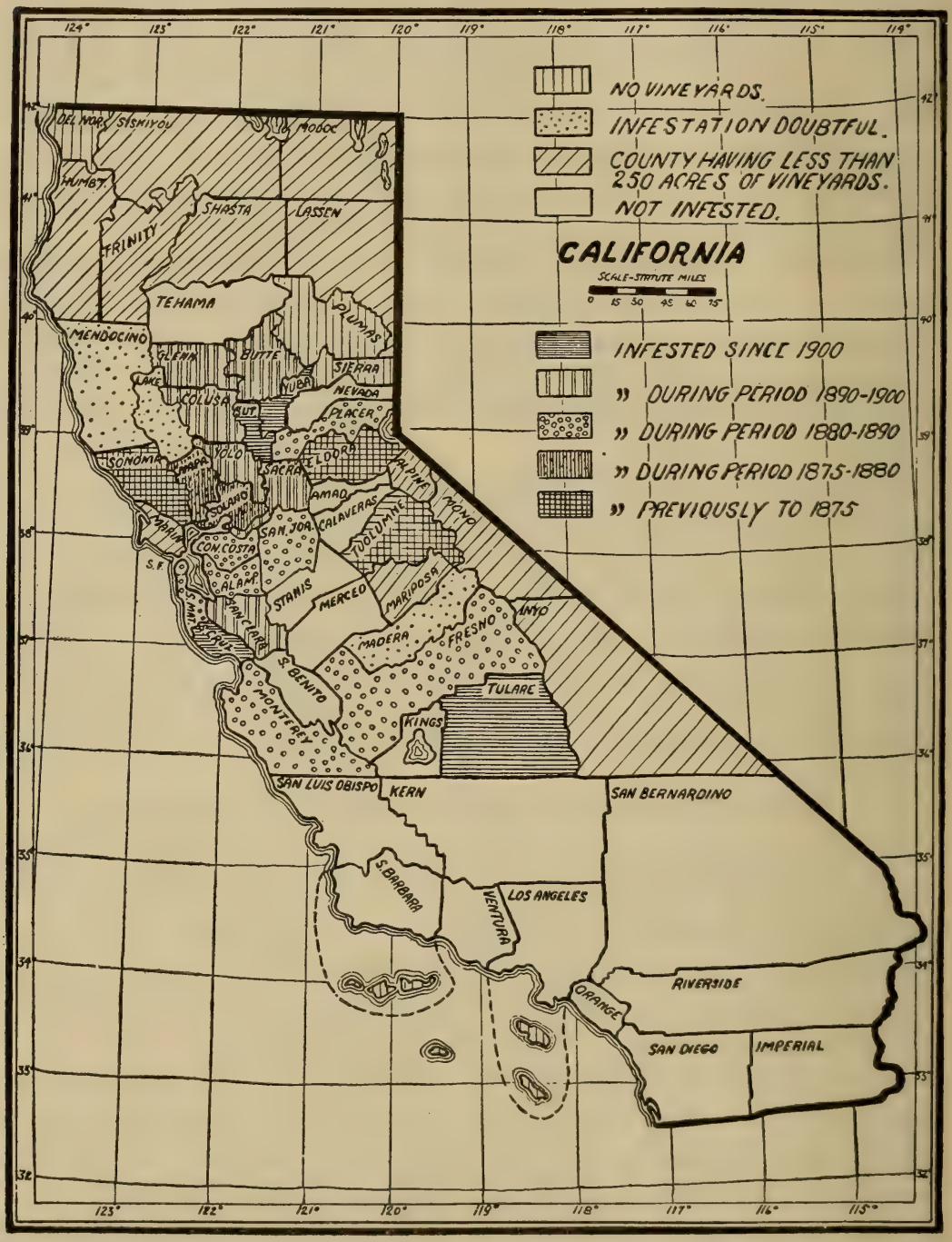


FIG. 1.—Map indicating progress of phylloxera infestation in California. The map does not show the severity or degree of infestation. Counties having less than 250 acres of vineyards were not inspected. In those counties marked doubtfully infested inspection took place at a time of year when the insect was difficult to detect; none were found but the aerial growth of the vines suggested phylloxeration. In the counties of Kings, San Benito, Merced, Stanislaus, Calaveras, Amador, and Tehama no phylloxera was found at the time of inspection, but they should not be deemed to a certainty free of the insect.

the State Board of Viticultural Commissioners and other agricultural and horticultural reports is presented. This, with the aid of a map of California (fig. 1) to indicate infested counties in shad-

ings to correspond to a period of years within certain dates, will enable one at a glance to conceive the degree of injury produced and the loss sustained by the viticultural interests.

A general idea can be formed of the growth of the viticultural interests of California and correlatively of the economic importance of the grape phylloxera by comparing the report on grape production of the State statistician for the year 1914 with the report of a similar nature for the period 1856–1866 (Table I).

TABLE I.—*Planting of vines in California in different perods.*

County.	Vines planted in—			Total vines existing in 1865.	Total bearing vines existing in 1866.	Total vines existing in 1910.
	1856	1857	1858			
Alameda	48,000	125,000	175,000	1,575,000	155,070	2,390,959
Amador	9,000	8,000	20,000	180,000	757,773	314,604
Butte	15,000	45,773	80,707	726,363	369,785	258,742
Calaveras	.....	6,465	24,187	217,665	515,049	212,300
Colusa	10,000	3,120	4,285	36,000	47,800	482,417
Contra Costa	75,000	34,468	42,640	383,760	201,518	2,972,130
Del Norte	.....	.....	1,056	2,450	120	.....
Eldorado	6,390	26,400	77,472	697,248	1,441,039	581,342
Fresno	2,000	1,000	3,000	27,000	.....	40,687,207
Humboldt	800	500	915	8,235	839	4,095
Inyo	.....	.....	.....	.....	252	39,478
Klamath	.....	1,000	2,000	18,000	2,917	.....
Lake	.....	.....	.....	.....	11,000	296,752
Lassen	.....	.....	.....	.....	200	31
Los Angeles	726,000	600,000	1,650,000	14,850,000	3,000,000	4,923,877
Marin	.....	500	600	5,400	11,542	115,198
Mariposa	1,000	15,227	15,000	135,000	51,783	28,647
Merced	10,000	15,000	15,000	135,000	100,740	1,281,342
Monterey	10,000	11,650	50,000	50,000	84,839	79,935
Napa	22,700	55,000	90,000	810,000	1,166,935	8,595,338
Nevada	.....	6,000	8,000	72,000	124,000	94,338
Placer	2,702	5,742	5,000	45,000	397,101	1,340,132
Plumas	.....	800	400	3,600	1,616	.....
Sacramento	52,200	119,500	327,900	2,951,000	951,315	7,627,510
San Bernardino	80,000	38,000	75,000	675,000	312,562	987,127
San Diego	4,000	4,000	50,000	450,000	1,915	1,228,858
San Francisco	.....	1,200	1,000	9,000	75	3,000
San Joaquin	13,467	28,640	40,000	4,112,792	493,387	13,371,794
San Luis Obispo	1,500	2,000	10,000	90,000	18,263	265,481
San Mateo	5,000	40,000	40,000	360,000	16,000	124,990
Santa Barbara	15,000	70,000	90,000	810,000	220,000	208,595
Santa Clara	150,000	500,000	513,000	4,617,000	2,000,000	5,584,480
Santa Cruz	5,000	6,179	20,000	56,000	218,100	1,365,418
Shasta	5,348	6,100	25,000	225,000	1,534,520	117,481
Sierra	.....	1,900	3,500	31,500	4,737	.....
Siskiyou	1,000	1,000	2,000	180,000	8,469	2,473
Solano	56,178	50,000	52,869	554,178	950,600	1,213,265
Sonoma and Mendocino	61,590	170,508	187,621	2,000,000	2,830,195	18,864,163
Stanislaus	4,420	3,020	1,800	162,000	112,310	1,932,302
Sutter	45,123	135,369	50,000	450,000	163,663	1,249,923
Tehama	.....	2,000	5,500	49,500	145,883	1,307,218
Trinity	150	1,717	1,151	10,359	19,096	2,842
Tulare	.....	400	30,000	270,000	100,950	7,227,491
Tuolumne	9,858	29,891	57,520	517,734	505,250	95,811
Yolo	26,902	61,903	155,425	1,398,825	157,434	2,568,019
Yuba	28,000	30,000	50,000	450,000	494,472	162,751
Alpine	.....	.....	.....	.....	.....	9,000
Glenn	.....	.....	.....	.....	.....	20,416
Imperial	.....	.....	.....	.....	.....	298,813
Kern	.....	.....	.....	.....	.....	419,582
Kings	.....	.....	.....	.....	.....	4,538,732
Madera	.....	.....	.....	.....	.....	795
Modoc	.....	.....	.....	.....	.....	2,000
Mono	.....	.....	.....	.....	.....	282,682
Orange	.....	.....	.....	.....	.....	1,570,794
Riverside	.....	.....	.....	.....	.....	177,976
San Benito	.....	.....	.....	.....	.....	1,530,630
Ventura	.....	.....	.....	.....	.....	36,398
Total number of vines	1,540,134	2,265,062	3,854,548	40,172,654	19,695,814	139,099,560
Total acres	.....	.....	11,411	59,077	28,966	.....

At this earlier period the pioneer growers of grapes were beginning to realize the possibilities of success due to the advantage of the peculiar suitabilities of climate and soil in California for the culture of European varieties of *Vitis vinifera.*

Within the period of 48 years (1866–1914) there had been an increase of nearly 90,000,000 vines. Within this lapse of time, so comparatively short for such a prominent industry of the State, many changes occurred in the different viticultural districts with which phylloxera had little or nothing to do, and the gradual damage and loss caused by the insect could not be compared with the acutely sinister influence of extreme fluctuations in the market values of grapes, whether for wine, raisin, or table use, which swayed the industry at different times from opulence to ruin and vice versa for the growers; yet when looking backward over the years, the phylloxera stands out preeminent and is considered as the main single factor in the loss and damage sustained by California viticulture.

In the early period the counties south of the San Bernardino boundary line were in the lead for the acreage in vines and for the production of wine. To-day in these counties viticulture is of secondary importance, yet phylloxera has never been discovered there. The Anaheim disease was one of the causes of this decline, but the change to the more lucrative investments in citrus culture, which no doubt appealed more to the tastes of the many eastern settlers who largely populated that portion of the State, is mainly responsible for the falling off in acreage of grapes and lack of interest in the industry.

Another viticultural district which underwent a great change was that of the Santa Clara Valley. There grape growing increased rapidly from 1885 to 1895, when the acreage of vineyards was the greatest and the county of Santa Clara produced almost one-third of the dry wines of the State. From 1893, when the vines began to die, the decline in acreage was much more rapid than had been its growth.

It was commonly believed at the time that the Anaheim disease, which had caused such great ravages in the southern part of the State, was also responsible for the sudden dying off of the vines in the Santa Clara Valley. The damage caused to the vineyards was so extensive that an investigation was instituted by the College of Agriculture of the University of California to determine the cause (3). The general conclusions arrived at were the following:

> First, that the dying vines exhibit symptoms differing materially from those shown by the vines in Southern California which were destroyed by the Anaheim disease; and, second, that whether or not there be some "unknown influence" at work, as suggested by Mr. Newton B. Pierce, the real, determining factor is the deficiency of rainfall during the years 1897–1900.

At this time the phylloxera was known to exist more or less throughout the valley, and had been identified in different vineyards, but as yet its injury had not reached the advanced stage of noticeable characteristic phylloxera spots, was therefore little in evidence, and was not considered a prominent factor in connection with the destruction of the vineyards.

The following facts were brought out during the writers' investigations and have a direct bearing upon existing conditions in the Santa Clara Valley at that time:

Extensive areas of a vineyard may be infested by phylloxera before characteristic spots are noticeable; a lighter crop and a slight decline in vigor of growth are for some time the only apparent signs of injury.

Infested vines change suddenly for the worse, becoming rapidly stunted in growth, or even dying, when influenced by unusual conditions either from lack or excess of moisture.

Injured roots, functioning poorly under normal conditions of moisture, reproduce with difficulty fibrous roots, or feeders, to replace those which have been destroyed by the insect, and when subjected to drought they starve the vine.

Excessive moisture, instead of benefiting injured roots, causes them to rot and hastens the death of the vine.

For these reasons it is believed that the phylloxera was responsible for a far greater share of the destruction of the Santa Clara Valley vineyards than has been ascribed to it.

While Santa Clara and the southern counties have lost in acreage, a larger gain has been made at about the same period and later in other counties, especially those of Sutter, San Joaquin, and Fresno. Many vines throughout the State have been killed by phylloxera and not replanted; more have been grubbed out and replanted, sometimes more than once, and it is estimated that the loss in these respects has been very considerable.

Mr. George C. Husmann, pomologist in charge of viticultural investigations, Bureau of Plant Industry, United States Department of Agriculture, estimates the loss at 75,000 acres; Prof. F. T. Bioletti, of the viticultural department of the University of California, makes a similar estimate; and Charles C. Wetmore, for many years identified with the board of State viticultural commissioners, considers this estimate conservative.

VINEYARD DESTRUCTION.

PROGRESS OF THE DESTRUCTION OF A VINIFERA VINE.

According to conditions there is a great variation in the number of months or years that elapse between its original infestation by

phylloxera and the actual death of the vine. The following points have important bearing on this:

Soil conditions and drainage.—From a survey made throughout the different districts of California, the following general statements can be made in regard to the destruction of vineyards when the vines are 8 to 10 years of age or older before becoming infested:

Vines live longer in rich, deep, well-drained soils. Under such conditions, vineyards known to have been infested for 20 years and longer still bear crops, have only a few vines actually dead, and but a small percentage bearing little or no crop.

Vines die sooner and the crop of the vineyard is more rapidly diminished in quantity and quality when established on rich soil only a few feet deep and with poor drainage, or on side-hill soils lacking moisture.

Vines are still more rapidly affected in heavy soils, more or less shallow, with compact clay subsoil. In such types of soil, the vines, more or less stunted and enfeebled, may live a number of years. After a winter of unusually heavy rainfall they may show a very rapid serious decline or even a majority of them may die within a year.

Vines growing in a well-drained, very loose, and friable sandy soil, or one with a surface of blow sand several inches in depth, seem to be almost immune to the attack of phylloxera.

As a sandy soil becomes heavier in texture and of poorer drainage, so the vine succumbs more readily to the attack of the insect.

Age of vine at infestation.—Young vines are destroyed more readily during the first three years, before they have established a fairly good root system. When vines are 8 or 10 years old the quality and texture of the soil become main factors, and the more or less rapid destruction of the vineyard depends on the adaptation of the vine to the soil and the advantages of prolification and diffusion for the insect. The general experience has been as follows:

Cuttings infested in their early growth rarely survive the first year.

Rooted vines, infested from the time of planting, produce from the start a very poor vineyard, which rarely lasts more than three or four years, the individual infested vines living after infestation hardly more than two years. If vines become infested during the second or third year from planting, they may last longer if they have a good root system, and in this case the vineyard may produce one or two crops smaller than normal and perhaps last five or six years. When a vine is three years old or more before infestation, its longevity depends somewhat on variety, much more on age, and especially on soil conditions.

Too few American varieties, either nonresistant or resistant, are grown in the State of California at this time to have been considered in this investigation.

Intrinsic vigor of vines.—Vines of great intrinsic vigor always resist phylloxera attack better than naturally weak plants.

Varieties of vines.—Amongst vinifera varieties grown in California, a few have shown certain resistance when inoculations have taken place several years after planting. Such are, in order, Flame, Tokay, Mission, and Muscat (Fresno district), and in a lesser degree Grenache, Chasselas, and Burger. Laboratory tests with certain varieties in which phylloxera lesions rotted rapidly have shown that Zinfandel, Thompson's Seedless, Carignan, Burger, and Muscat succumbed more rapidly and Tokay and Grenache less rapidly.

Destruction of a highly susceptible vine.—Under favorable conditions for rapid phylloxeration, the hypothetical progress of destruction of a highly susceptible vine, as Zinfandel, with established roots may be set down as follows: During summer and fall a few larvæ settle on a part of the root system; the following year infestation spreads to the surface fibrous and fleshy roots, and to a certain extent to the large roots near the crown, and nodosities and tuberosities are formed. The third year the subterranean infestation spreads pretty well throughout the root system, although it is rare to find year-old wood much attacked, for it appears that the habit of roots of this age to slough the outer layer of bark prevents the phylloxeræ from retaining a hold, and compels those already settled to move to other more hospitable portions of the root system. In this year some of the larger roots decay under combination of phylloxera attack and excessive moisture in the subsoil or become dried out from phylloxeration combined with too great drought, and thus the flow of sap between the feeding rootlets and the aerial portion of the vine is more or less cut off. This results in a shortening of cane growth and sometimes in an abnormally large crop of grapes. During this third summer as the larger roots die an emigration of young larvæ takes place. Many winged forms also may be developed. The fourth year finds the larger roots in great part destroyed, the cane growth correspondingly reduced, and a large number of fibrous and fleshy rootlets sent out from the trunk just below the soil surface. The phylloxeræ colonize these rootlets in spring, but leave them in summer, when they decay. There is also a heavy migration from the decaying roots farther down in the soil. In the autumn it is hard to find phylloxera on such a vine, and this explains the maxim that the best type of phylloxerated vine on which to look for the insect is not one badly stunted, but rather one with slight stunting of the canes; in fact, one in the

second or third year of phylloxeration. Such a vine as has been portrayed generally dies in the fifth or sixth year from the initial attack.

As has been pointed out above, the decline of a vine is influenced by many conditions, and the hypothetical case given shows the minimum longevity of an established susceptible vine after phylloxeration. Under favorable conditions infested vines live much longer, and in extreme cases their length of life seems hardly affected by the continued presence of the insect on their roots, a slight decrease in the size of the crop being the only evidence of injury.

HOW THE PRESENCE OF PHYLLOXERA IS INDICATED.

The existence of the phylloxera in a vineyard is indicated by the well-known areas or "oil spots," so termed because of their manner of spreading. A "spot" appears first in the form of one or two vines showing a slight shortening of the canes and a premature seasonal yellowing of the leaves, although the latter symptom may be caused by the red spider (*Tetranychus bimaculatus* Harvey), or by alkali in the soil. The year following this indication the vines originally infested exhibit a more noticeably stunted appearance, while other vines surrounding them show slight shortening of canes and premature discoloration of foliage. After this the "spot" increases in size, in course of time the vines in its center die, and finally the vineyard may become totally destroyed. The writers have never observed the "spots" to increase as rapidly in California as they are reported to have done in the vineyards of France after the time the insect first reached that country, when 2,500,000 acres were destroyed in 25 years, and vineyards frequently have been observed in California which had phylloxera "spots" of more than 20 years' standing to have vines still living.

The "oil spot" generally is circular in shape, but sometimes it assumes other forms. At times it is oval or narrowly elongate, the latter form occurring on hillside vineyards through which water rills run in the spring. In such cases spread of the "spot" is often rapid in a downward direction, indicating that running water is an extra factor in the spread of infestation. The writers have demonstrated by experiment (see "Diffusion of phylloxera," p. 100) that the phylloxeræ can be carried in water from one vine to another, and when the rains of March and April occur there are plenty of active phylloxeræ on the roots. In other cases the spread of a "spot" follows the direction of the prevailing winds and it appears that this spread is caused by wind agency in the transportation of wandering larvæ in summer and autumn. In vineyards where vines are planted rectangularly (i. e., 8 by 12 feet), instead of square, the infestation

very frequently spreads along the shorter 8-foot rows, indicating that the insects traverse more easily the shorter than the longer distances. Aerial and subterranean migrations of wandering larvæ play an important part in the enlargement of phylloxera "spots." Only an infinitesimal percentage of the thousands of wandering larvæ succeed in reaching their goal, but, as they are parthenogenetic radicicoles, a single larva can cause a new infestation or start a new "spot" at quite a distance from the original one, either in the same or in another vineyard.

The estimation of root injury from external appearance usually can be made with considerable accuracy, and the degree of infestation of a vineyard computed by the number of "spots," their size, and the stunted condition of the vines composing them.

The diagrams (figs. 2 and 3) indicate a phylloxera "spot" charted, respectively, in the years 1914 and 1915. This "spot" occurred on a heavy black clay soil on a hillside of moderate slope. It appeared that the "spot" started about the year 1907 when the vines were 3 years old, and that the first vines died about 1911. Surveys of the "spot" were made October 13, 1914, and November 5, 1915, and the vines were designated in the following manner: Ten was given to vines which showed no external evidences of phylloxeration; 9 to those which showed very slight evidence, such as premature yellowing of foliage and slight shortening of canes; 8 to those showing more advanced symptoms of phylloxeration, and so on down to 1, which was given to vines which showed only the most feeble vegetative growth. In order to portray the "spot" more vividly, symbols have been utilized as follows: Healthy vines, *H*; vines designated 9 and 8, *S*; vines designated 7 and 6, *I*; vines designated 5 and 4, *U*; vines designated 3, 2, and 1, *D*; vines killed by phylloxera, solid dot. In this vineyard every fourth vine had been replaced by a walnut tree, and these places where vines have been pulled out and not replaced are left blank in the diagrams.

In the diagrams not all the "spot" is shown, for it has extensions, the principal one being on the north side across a 24-foot avenue and continuing down a swale for some 60 feet. Enough of the "spot" is shown to indicate its general form. Between 1914 and 1915 there occurred an unusually wet winter and the "spot" grew considerably in the 12 months between the surveys. Although the number of dead vines increased only from 43 to 49, and among the badly stunted types not much increase was shown, there was a marked increase in the number of vines showing recent phylloxeration.

When more than one variety of vine is included in a "spot," a good index of the resisting power of the several vinifera varieties frequently is observable. Among the dead or moribund vines of

the susceptible varieties stand out the more vigorous vines of the less susceptible kinds or even individuals of the same variety.

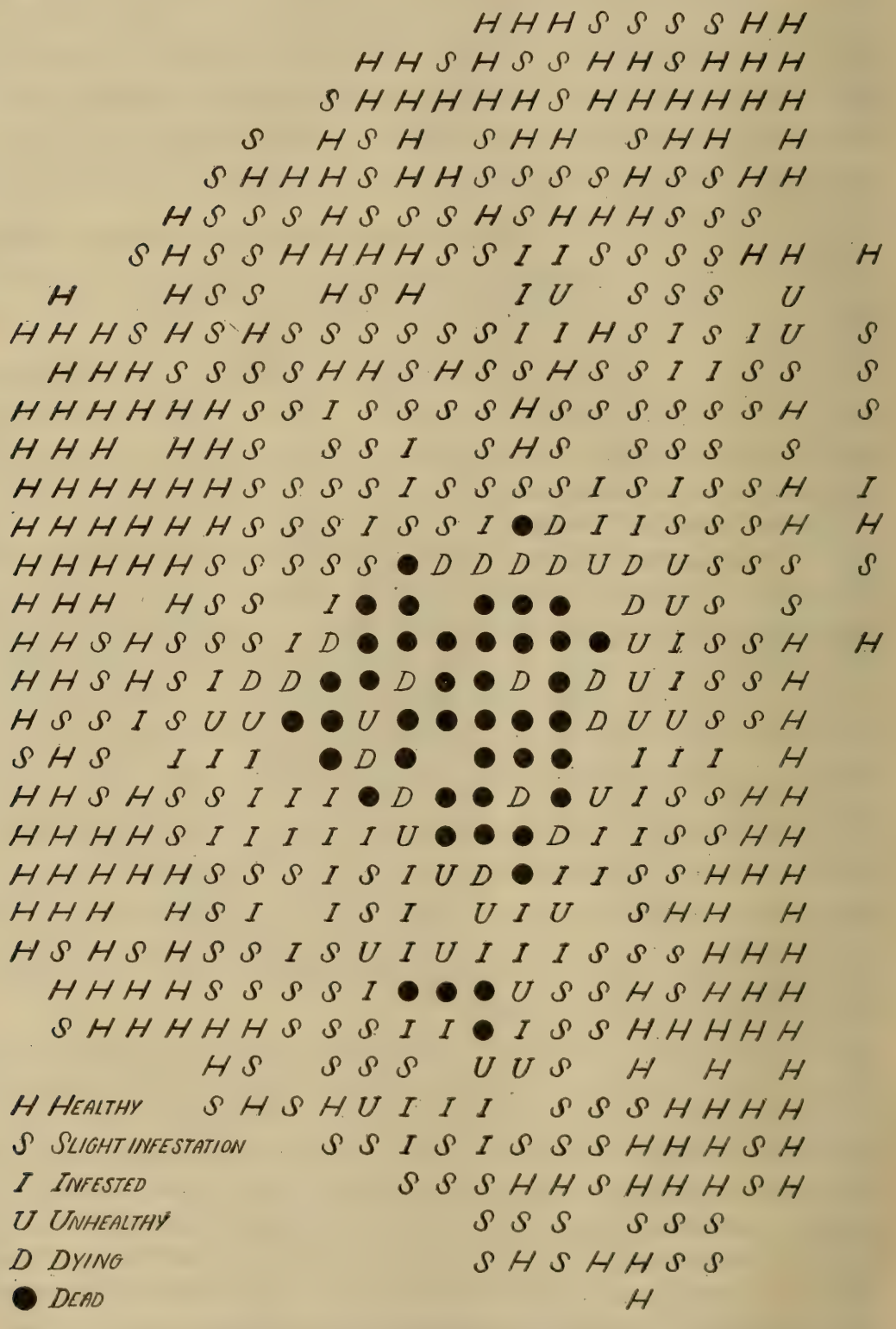


FIG. 2.—Phylloxera "spot" in Zinfandel vineyard, charted in 1914. (See text.)

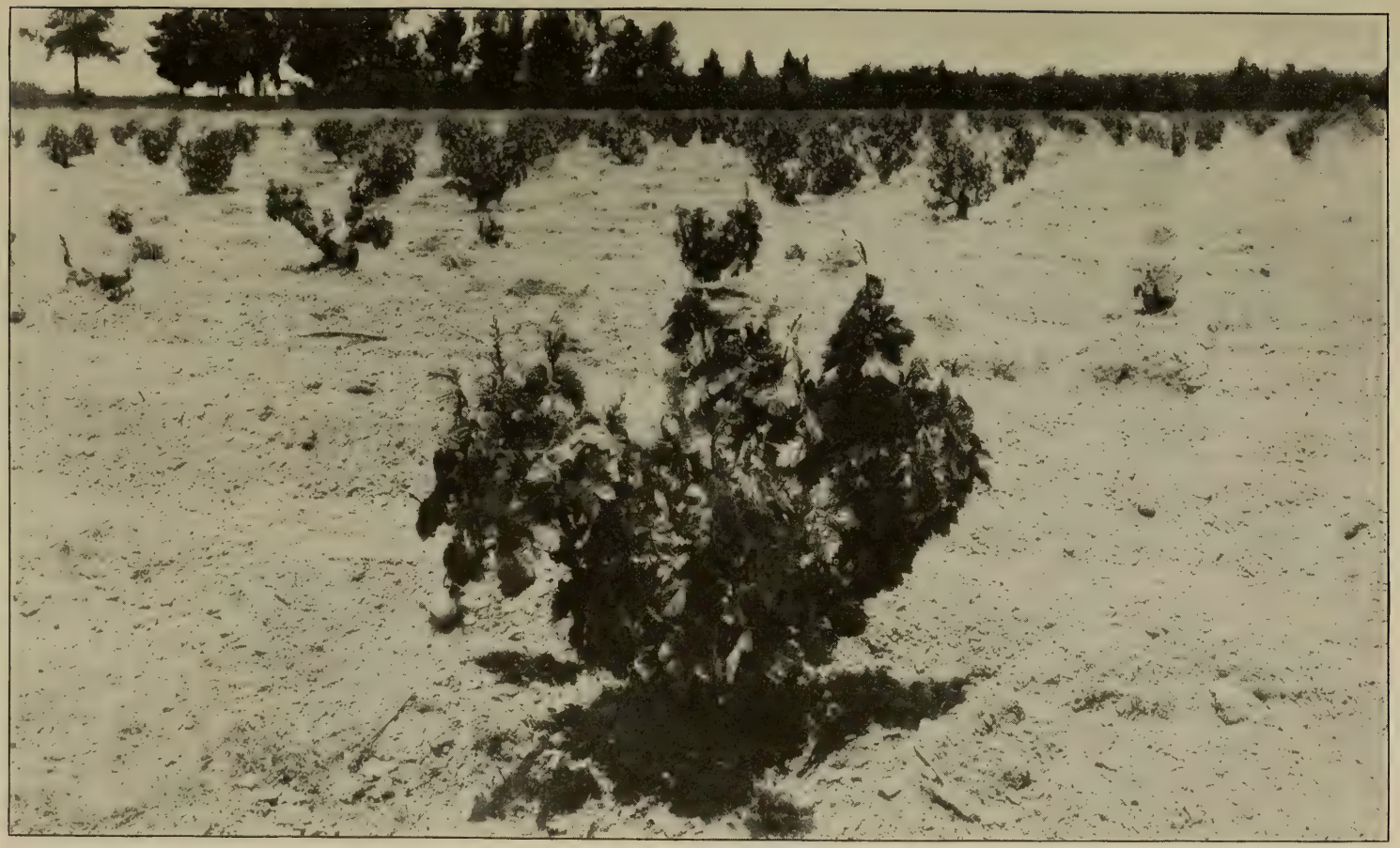
The year previous to showing a marked decline, vines frequently bear an unusually abundant crop of grapes, and stunted vines seem to produce a larger amount of grapes in comparison to the size of

FIG. 1.—Young raisin vineyard uninfested by Phylloxera.

FIG. 2.—Old vinifera vineyard infested throughout with Phylloxera and showing empty spaces where vines have been killed; vine in foreground shows less infestation by Phylloxera than others near by, and would be rated at 7, but the canes show obvious stunting.

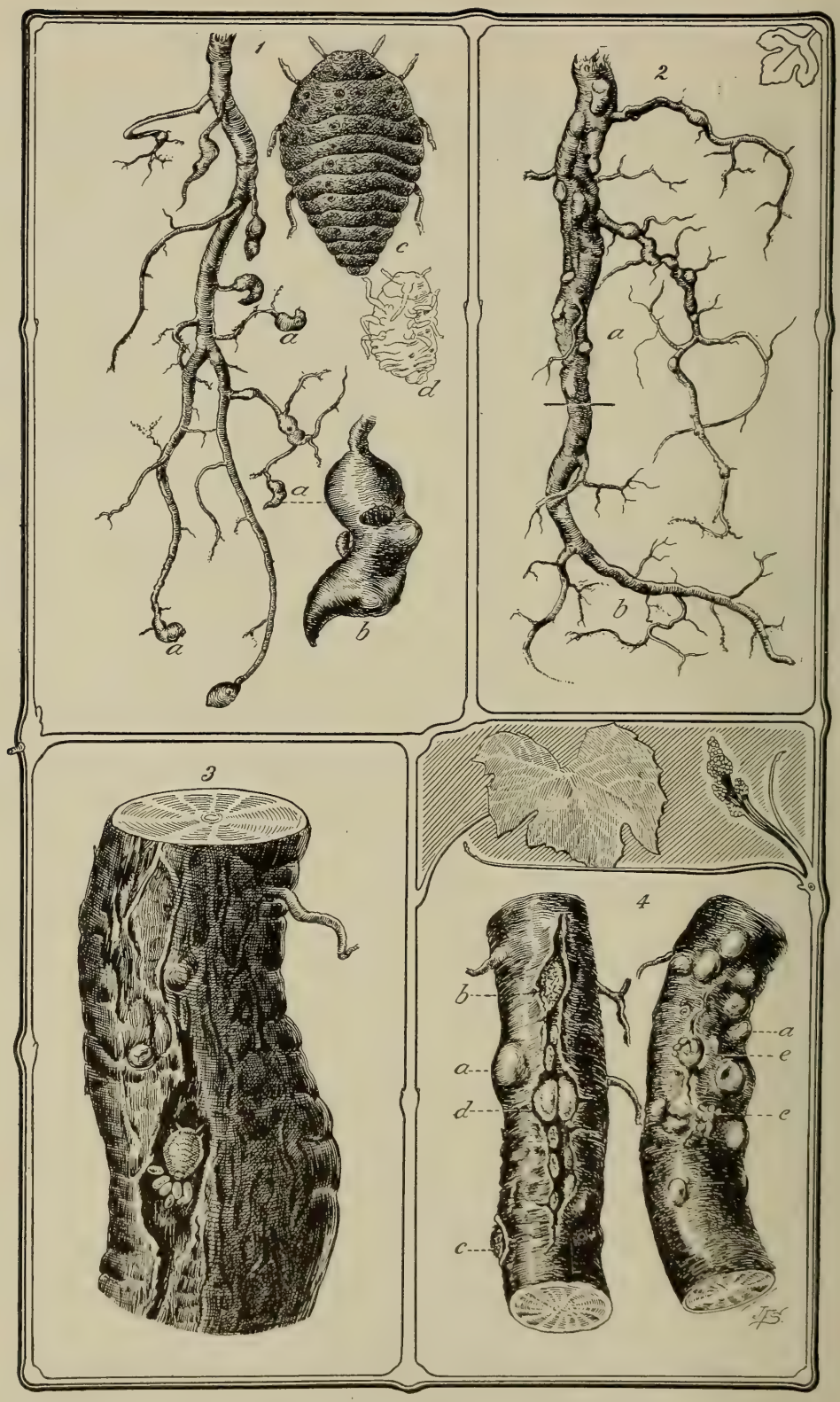
THE GRAPE PHYLLOXERA IN CALIFORNIA.

Old Tokay vineyard with Phylloxera infested "spot" in foreground; vine in central foreground to be rated at 6; the two vines on sides in foreground to be rated at 3 on the scale of Phylloxera injury.



THE GRAPE PHYLLOXERA IN CALIFORNIA.

Old vinifera vineyard infested throughout with Phylloxera, and showing many empty spaces where vines have been killed. None of the vines in the foreground is to be rated above 3 on the scale of injury from 1 to 10.



THE GRAPE PHYLLOXERA IN CALIFORNIA.

Phylloxera vitifoliae: Fig. 1.—Phylloxera nodosities shown on Zinfandel grapevine: *a*, Nodosities on terminal rootlets; *b*, nodosity showing Phylloxera feeding; *c*, adult louse; *d*, molted skin of same. Fig. 2.—Phylloxera tuberosities on smaller root: *a*, Infested portion of root; *b*, normal portion of root. Fig. 3.—Section of grapevine root showing adult louse with eggs *in situ*. Fig. 4.—Sections of root infested: *a*, Newly formed tuberosity; *b*, advanced stage of tuberosity; *c*, side view of older form of tuberosity; *d*, tuberosity causing the cracked condition of bark; *e*, young colony of insects as found on roots.

their wood growth than do healthy ones. Such grapes mature, however, without attaining a good size or their normal saccharine con-

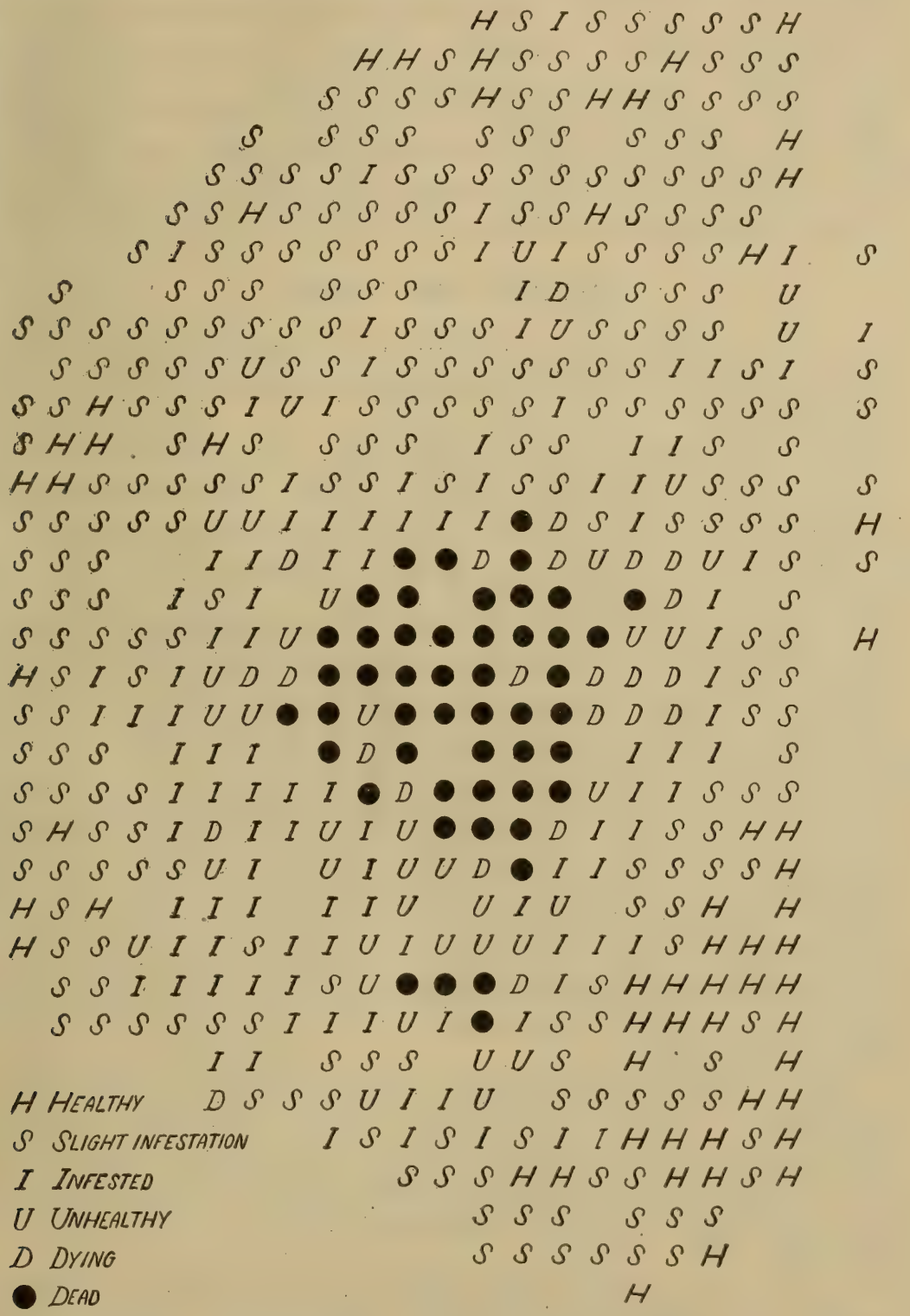


FIG. 3.—Phylloxera "spot" in Zinfandel vineyard, charted in 1915. Same "spot" as shown in figure 2. (For description see text.)

tent. Stunted vines produce leaves of a more uniform size than healthy vines, and because the internodes of the canes are shorter, the leaves appear more closely grouped, giving the "cabbage-head"

appearance to the vines. Scarcity of rapid-growing terminal shoots and absence of tendrils are characteristics of stunted vines. Plate I, figure 1, shows a young vineyard which is uninfested and in which the vines have made normal growth. Plate II shows a small phylloxera "spot" in an old vineyard, the photograph showing stunted vines in the foreground. Plate III and Plate I, figure 2, indicate badly infested old vineyards, in which all the vines are phylloxerated and most of them badly stunted. The vine in the foreground of Plate III is obviously stunted, although less so than its neighbors.

PHYLLOXERA ROOT LESIONS.

Root lesions are swellings on grape roots caused by the puncture of the phylloxera beak. They are of two types, (1) nodosities and (2) tuberosities.

The nodosity.—Nodosities (Pl. IV, fig. 1) are rapidly growing swellings on the white fleshy feeding rootlets. They soon acquire a characteristic greenish-yellow color, and curve and bulge around the phylloxeræ responsible for their inception so that the insects come to lie in a depression (Pl. IV, fig. 1, *b*). A nodosity may become as much as six times the diameter of the normal size of the root when several insects have settled upon it, and about twice the diameter for a single occupant. Through its size, form, and color, the nodosity is very conspicuous in comparison with the root and is manifest proof of the presence of the phylloxera.

In most cases the formation of a nodosity arrests the growth of the rootlet. At times the rootlet grows one-fourth inch or so in length, and occasionally the puncture of the phylloxera does not affect the rootlet in its growth, the subsequent swelling acquiring a lignous character and becoming a tuberosity. Nodosities are generally short-lived, lasting about a month. Excess moisture hastens their decay, lack of moisture dries them up, but a low, even temperature causes them to last longer.

The foregoing also applies to the American variety of vines styled nonresistant. On the rootlets of the resistant American vines the phylloxeræ frequently fail to cause swellings, and when nodosities are produced they are smaller, less fleshy, and brown in color. At times, though no swelling occurs, the rootlet dies at the point of puncture.

The tuberosity.—Tuberosities (Pl. IV, figs. 2, 4) also are swellings caused by the puncture of the aphid. Though of a similar nature, they differ from nodosities in form because of the lignous character of older roots. They occur on all parts of the root system of vinifera vines except at the apex of the growing fibrous rootlets. They may

also occur on the trunk of the vine, both above and below the soil surface. They are less commonly formed on roots of one year's growth than on older wood. On resistant vines tuberous swellings are normally quite unusual, but they may be formed on the healing growth of the cambium layer about an abrasion. On most American vines of nonresistant type, tuberosities are abundantly formed. On vinifera×resistant hybrids the more the resistant strain predominates the scarcer are the tuberosities.

Tuberosities are formed at any time between March and October, most abundantly during the summer months. They are formed more readily on vigorous roots than on those somewhat dried or decayed. Hibernants often choose tuberosities upon which to pass the winter, besides inducing their growth at points as yet sound and uninfested, the mere insertion of the beak being sufficient to stimulate growth. Tuberosities vary considerably in their general appearance, even on the same vine. Some are minute papillæ on the surface of the root. Others are large, fleshy, rapidly growing, globular outgrowths, as much as half an inch in diameter, and this type is found chiefly on the smaller roots. Others are enlargements of the girth of the root at intervals, a type also confined to small roots. Others consist of more or less uniformly rounded swellings of one-sixth to one-fourth inch diameter on the root surface, and these are the ones most commonly found on larger roots. Such tuberosities by their growth generally split the epidermis of the root longitudinally, and as the split tends to lengthen at both ends, the tuberosity assumes an oval or elongate shape. Later, when the split enlarges, fresh tuberosities are formed by aphids on the inner layer of bark exposed by the split, and shortly a chain of lesions occurs along the crack. These cracks lengthen and often involve a length of more than 6 inches. On roots growing horizontally or almost parallel to the soil surface, the majority of the tuberosities will occur on the lower side, the insects apparently settling there because of the greater moisture. On vertical or sloping roots tuberosities occur more or less uniformly all around. As long as they remain fresh, tuberosities provide an excellent quality of food for the aphids. This condition should be distinguished from the rapid development observed in the case of aphids settled on root callus, which forms at the point of severance and is caused by the action of the healing cells of the cambium layer becoming greatly enlarged and very fleshy, furnishing excellent food for the aphids, through the natural function of the wounded root.

Many factors influence the length of existence of tuberosities. In general, it is found that those formed in the autumn will last until the rainy season, and commence to decay immediately afterwards.

Their decay is expedited by a heavy rainfall and a high-water table. Those formed during the spring and summer in a moist environment rarely persist fresh beyond two months, and most of them decay about one month after they arise. It has been repeatedly observed how quickly a fresh tuberosity decays when it is placed against wet sand, and if a stream of water finds its way down a root the tuberosities thereon start to decay immediately. On the other hand, they are more capable of withstanding dry soil conditions than are the nodosities, and under conditions approaching drought, which sometimes occur in late summer and autumn, may last for a considerable time and even lignify, the dry environment having caused the insects settled on them to seek more favorable conditions of moisture and at the same time having kept in check decomposition. Tuberosities withstand a considerably greater range in temperature than do nodosities, and they are not affected by sudden changes in temperature in the same manner as are the nodosities.

Tuberosities grow larger and more rapidly in proportion to the soundness of the roots. On roots previously uninfested the growth of the swellings is rapid and vigorous, and a root, after it has been heavily phylloxerated for several months, becomes so greatly exhausted that it can not respond to the punctures of the aphids by developing new swellings, and the phylloxeræ that are not gradually driven away to seek more nutritious food develop on the root without causing swellings. The decay of the tuberosities begins at the place first punctured by the aphids, generally at about the center of the swellings. The tuberosity forms around the insect, and decay is first evident as a small, blackened spot, sometimes exuding a liquid. The rapidity of decay of tuberosities is in proportion to the increasing moisture content of their environment, and in an unusually dry environment they frequently will lignify without causing the tissues to rot. Under moist conditions the inflated cells rapidly break down and decay usually spreads, and fungi and molds enter the tissues, especially in the case of large bulbous swellings. Decay finally drives off the aphids, but through their stimulating action they are often able to retain the freshness of a tuberosity for some time after it has been surrounded by decayed tissues, and occasionally a fresh, vigorous specimen is found on a root otherwise quite decayed. The nutritious quality of these tuberous lesions provides for the production of nymphs in great numbers.

HOW ROOT LESIONS AFFECT THE HEALTH OF VINES.

It has been shown in the foregoing pages that the nodosities are those phylloxera lesions formed at the apex of growing fibrous rootlets, whereas the tuberosities are lesions formed on all other parts

of the root system. Since the vine derives its plant food through the growing rootlets that thrust their way through the soil, it is obvious that when such rootlets rot as a result of the decay of the nodosities situated on them no more sustenance can be afforded the plant through this medium. If, on the other hand, the rootlets continue to grow notwithstanding the nodosities situated on them, and if the nodosities lignify, the supply of nourishment provided by the rootlets is not cut off, and the nodosities become in effect tuberosities. This is often the case with resistant vines, and much more rarely with vinifera or nonresistant Americans. In resistants these tuberosities generally lignify and heal, but in the other types of vines they do this only if their environment is quite dry. Nodosities effectively destroy the terminal rootlets; but since the insects spread very slowly on resistants, a vine of any vigor has abundant feeders, and thus it follows that resistant vines bearing very few or no tuberosities, but having many nodosities, do not succumb to phylloxera. Resistant vines never lack the power to produce enough feeding rootlets to sustain them as long as the following conditions, which are normal to these vines, obtain: (1) When the development and spread of the phylloxeræ on them are comparatively slow; (2) when a large percentage of insects that have been raised on the nodosities become nymphs and later leave the roots as winged migrants, in an endeavor to reach the surface of the ground or the aerial parts of the vines. Both of these conditions may be affected by the quality of plant food, as will be shown. Instances have been seen in which young resistant vines have been rid of their entire infestation because all of the immature phylloxeræ became winged migrants in the autumn, but in the majority of cases of infested resistant vines under observation there remained in late fall a small wingless infestation, and in some instances where the vines had been growing in small pots with insufficient nourishment infestations of wingless aphids persisted, and the production of winged migrants during the autumn was proportionately small. These wingless infestations, however, were not prolific. It appears that thrifty resistant vines afford poor nourishment for phylloxeræ, and they do not respond to phylloxeric irritation by producing swellings. When, however, resistant vines become weakened through a poor supply of plant food, the phylloxeræ attacking them persist and the vines respond to the phylloxeric irritation and form lesions.

Although the decay of the nodosities on vinifera vines destroys the feeding rootlets, this in itself is not a potent factor in the destruction of the vines by phylloxera. Except under abnormal conditions, such as the confinement of vines in pots with impoverished soil, no case has ever been observed in which the death of a vine could be attributed solely to the decay of nodosities, whereas instances have

been observed wherein vines flourished with their vitality but slightly impaired, notwithstanding a nodositous infestation extending over several years. One such instance was that of a 20-year-old vineyard of Burger and Chasselas (viniferæ) near Napa, Calif. In 1913 the vines had been phylloxerated for upward of eight years, and each year the nodosities had been extremely abundant and practically no tuberosities had been developed, yet the vines appeared quite thrifty, owing to the maintenance of a sufficient number of uninfested feeders. It is the decay of the tuberosities on the larger roots, which the vine can not replace, that causes at first the impairment of the vine's functions and later results in its death. The simultaneous decay of many tuberosities is the cause of rapid decline in the vigor of a vine and is the prelude to the vine's death. The larger roots near the crown of the vine are especially susceptible to tuberositous decay, while the decay of a root below the crown is often very slow. This lower portion under favorable conditions is able to maintain itself undecayed for months, if not years, and is capable of providing nourishment for phylloxeræ. It is frequently observable that vines retain their vigor despite a ring of decay at the crown of the roots, and do not become stunted until the major portions of the larger roots have rotted.

In a discussion of the effect of root lesions on the health of vines, emphasis should be placed upon the decay of the tuberositous lesions and upon the fact that this decay is invariably hastened by moisture and retarded by dryness. Decomposition is often hastened by the work of fungi, molds, thysanurans, and tyroglyphid mites. The most common mite so working is *Rhizoglyphus elongatus* Banks, specimens of which were determined by Mr. Nathan Banks. It is a rather large species and is very prevalent throughout the grape sections of California. It was frequently reared on decaying roots kept in the cellar of the laboratory. The mite is hyaline white, with two brown circular spots, one behind the other, on the dorsum of the abdomen.

NOMENCLATURE AND SYNONYMY OF THE GRAPE PHYLLOXERA.

The genus Phylloxera was erected in 1834 by Boyer de Fonscolombe (10). The type species is *P. quercus* de Fonscolombe. In 1856 Asa Fitch (9) described the grape-leaf gall louse as *Pemphigus vitifoliae*. The species was obviously placed in the wrong genus. In 1867 Shimer (21) erected a new family (Dactylosphaeridae) and a new genus, Dactylosphaera, for a new species of his (*globosum*) and tentatively placed *vitifoliae* Fitch in this new family and genus. In a footnote he also proposed the genus Viteus for Fitch's insect. In 1868 Planchon (20) described the grape root louse from France as *Rhyz-*

aphis vastatrix Planchon, and in the same year Signoret (22) placed the species *vastatrix* in the genus Phylloxera de Fonscolombe. The year following Westwood (23), in England, described the insect as *Peritymbia vitisana*, but in a later article the same year he placed his species in synonymy as follows: *Peritymbia vitisana* Westwood= *Pemphigus vitifoliae* Fitch, *Dactylosphaera* (?) *vitifoliae* Shimer, and *Phylloxera vastatrix* Planchon (19). Until 1900 the name generally recognized by writers had been *Phylloxera vastatrix* Planchon. In 1900 Del Guercio (12), in Italy, erected the genus Xerampelus to receive the grapevine species, which he therefore called *Xerampelus vastator*. This genus has not been recognized by all later authors. Grassi (11, p. 12) would retain Shimer's proposed genus *Viteus* as a subgenus to *Phylloxera*, and would thus name the species *Phylloxera* (*Viteus*) *vastatrix*. The present writers are inclined to retain the specific name *vitifoliae* Fitch on account of its evident priority over Planchon's more widely known *vastatrix*, and notwithstanding the objections raised by authors as to its orthographical correctness (*vitisfolii* and *vitifolii* have been preferred and written). As to the generic title, it has been decided that *Phylloxera* will be retained, the question of the subdivision of the genus being left to those who have had more opportunity to study the specific ramifications of this group.

The synonymy of the grape phylloxera as understood by the writers is therefore as follows:

Phylloxera vitifoliae (Fitch).

Pemphigus vitifoliae Fitch, 1855–56.
Dactylosphaera (?) *vitifoliae* (Fitch) Shimer, 1867.
Viteus vitifoliae (Fitch) Shimer, 1867.
Rhyzaphis vastatrix Planchon, 1868.
Phylloxera vastatrix (Planchon) Signoret, 1868.
Peritymbia vitisana Westwood, 1869.
Xerampelus vastator (Planchon) Del Guercio, 1900.
Viteus vastator (Planchon) Grassi et al, 1912.

BIOLOGY OF THE GRAPE PHYLLOXERA IN CALIFORNIA.

THE LIFE CYCLE.

The complete life cycle of the grape Phylloxera under natural conditions, i. e., on the wild vines of eastern North America, is extremely complicated (fig. 4). It is not the intention of the authors to enter into all the ramifications of this cycle in the present paper, but it may be said that the following are the main forms that occur: (1) The stem mother or fundatrix, which hatches in spring from the winter egg, ascends to an early leaf, settles on the upper surface, and causes to form around her a pocketlike gall opening on the

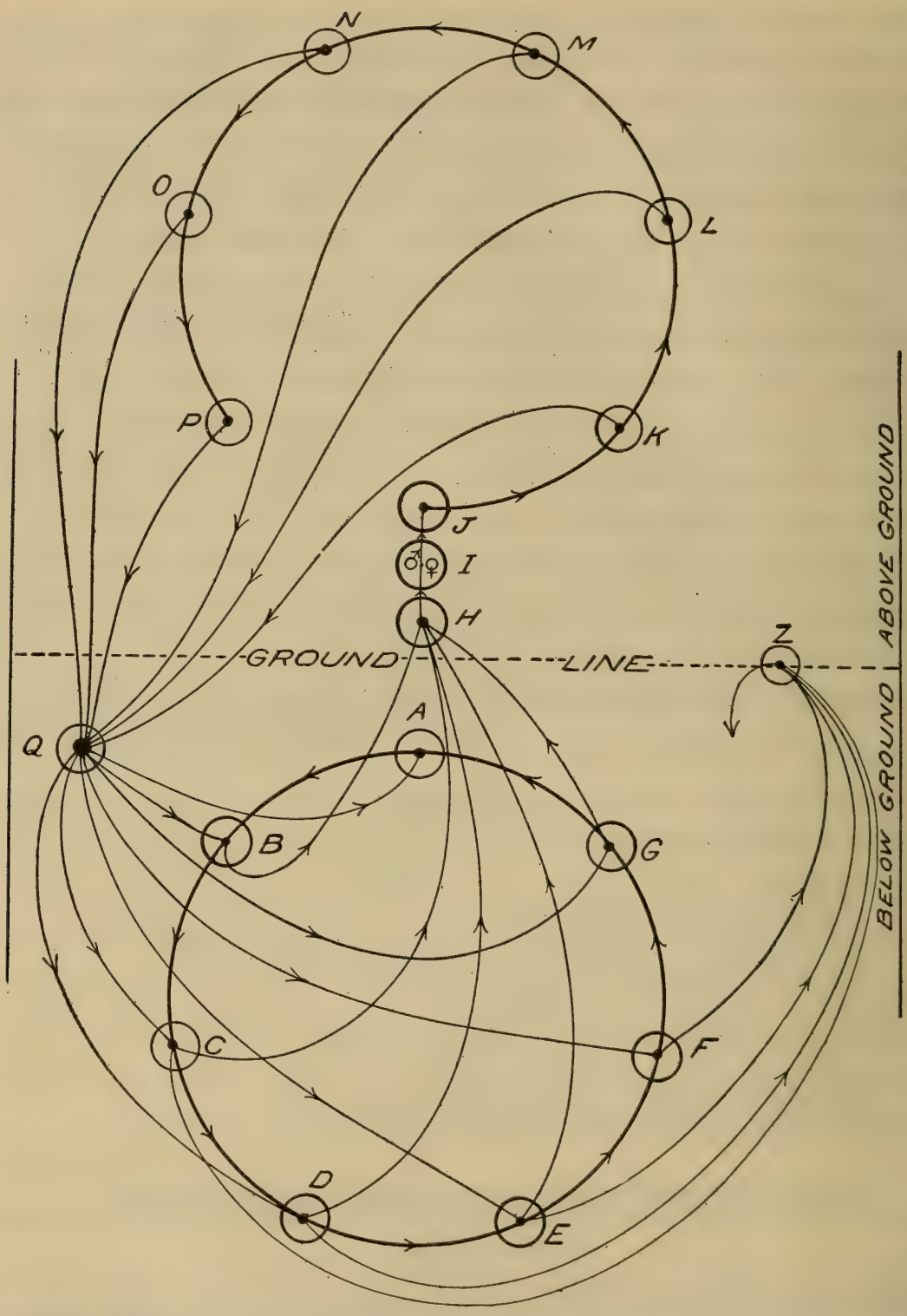


FIG. 4.—*Phylloxera vitifoliae:* Genealogical graph of the grape phylloxera in the eastern part of North America and in the Mediterranean regions. *A*, Hibernant radicicole; *B–G*, successive radicicole generations; *H*, winged sexuparous migrant; *I*, sexes; *J*, stem-mother gallicole; *K–P*, successive gallicole generations, part of the young larvæ of which proceed below ground (*Q*) to join the radicicole circle at various stages dependent upon the gallicole generation of which they were members; *Z*, emergence above ground of the wandering radicicole larvæ. In this figure, in order to avoid undue confusion, no account has been taken of the development in the galls of winged sexuparous migrants. Such development is unusual, but it indicates the possibility of a life cycle entirely aerial.

upper side of the leaf; (2) several parthenogenetic generations to which the stem mother gives rise, some of which settle on the foliage and produce new galls, as gallicoles, while others repair to the roots and settle on them as radicicoles; (3) parthenogenetic generations on the roots descended from the phylloxeræ which went from the foliage to the roots; (4) winged migratory forms, comprising a very variable percentage of the root and gall forms, produced in summer and autumn, which fly or are transported by wind to other vines and oviposit either under the bark or on the leaves; (5) the true sexes, which are wingless and beakless; (6) the winter egg, deposited under the bark by the sexed female after coition; (7) radicicoles, born on roots in the late autumn, which pass the winter thereon as small hibernants, mature the spring following, and give rise to radicicole generations which succeed one another during the summer and autumn. This, briefly, is the life cycle that occurs in parts of Europe where American vines are used for stock, and in the eastern and southern United States on the wild grapes and on varieties derived from them.

It will be observed that the winter may be passed in two forms—the winter egg and the hibernant, the former on the aerial and the latter on the subterranean or root portion of the vine. On certain wild grapes, as *Vitis riparia*, *V. rupestris*, and *V. berlandieri*, and on hybrids from these species, the former is the normal form, and hibernating larvæ are rare. On species like *Vitis labrusca*, *V. monticola*, and their derivatives, both forms may occur. On viniferæ (*Vitis vinifera*) the latter form is by far the more common. In the majority of European grape districts both forms occur, the former on American resistant vines and the latter on viniferæ, but in other localities, even where resistant vines are used, the winter egg is very scarce. These include certain regions of France and California, and it appears that in California the hibernant is normally the only form that passes the winter.

The suppression of the winter egg, and, therefore, of the succeeding gall form, brings about a modified life cycle in the California vineyard which may be briefly described as follows: (1) The hibernant radicicole passes the winter as a larva on the roots and occasionally on the trunk beneath the bark. (2) The hibernant, when mature, gives rise to generations of radicicoles, and the aphids that issue from eggs in late autumn become hibernants. (3) A certain percentage of radicicoles, varying from causes such as humidity, temperature, condition of food, and variety of vine, develop into winged migrants and issue from the ground. (4) Radicicole larvæ forsake the roots and seek to reach other vines either by way of the soil surface or through subterranean passages such as cracks.

The part of the life cycle from the sexes to the gallicoles through the winter egg and fundatrix is either omitted or does not proceed beyond the winter egg in California, notwithstanding the frequent

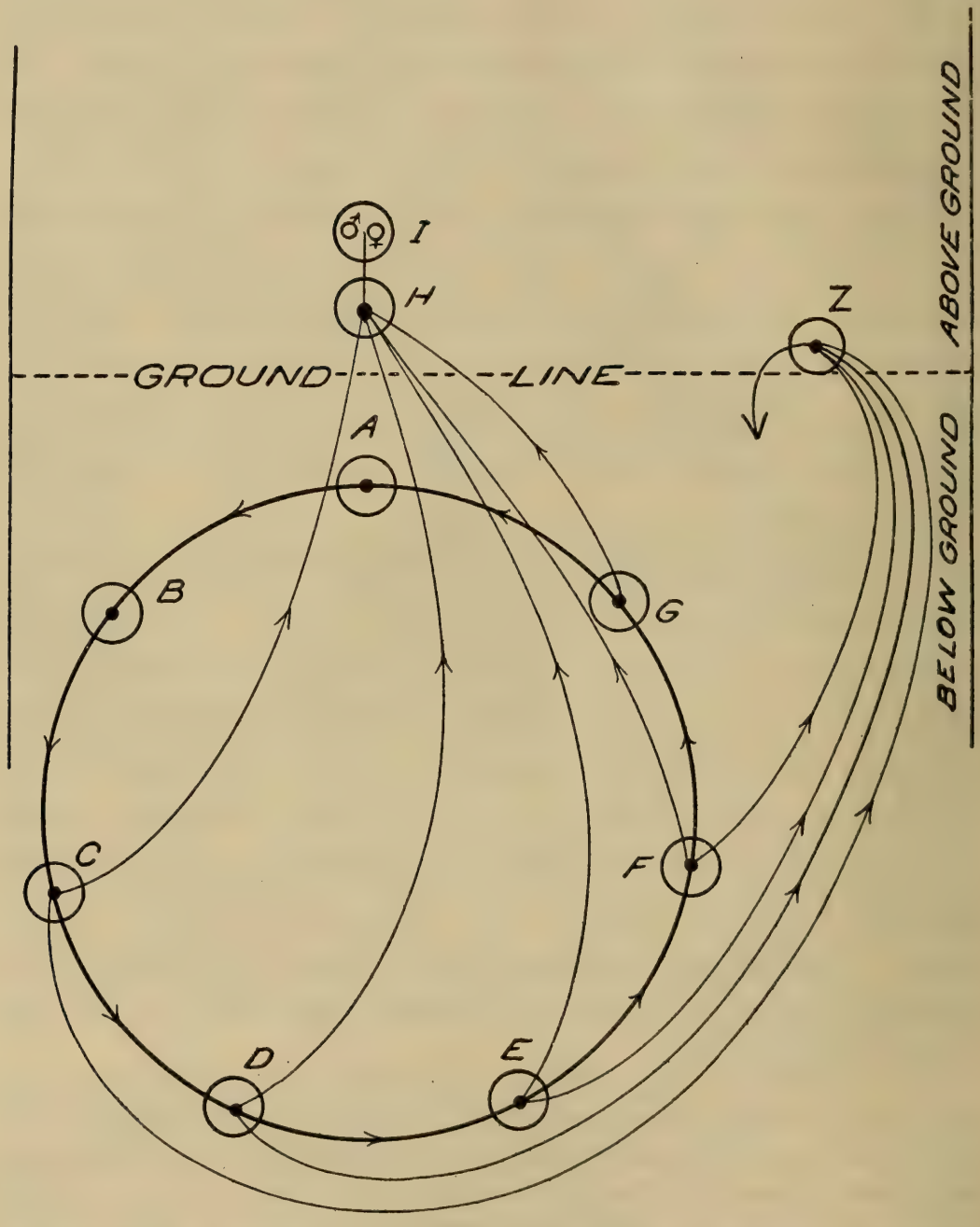


FIG. 5.—*Phylloxera vitifoliae:* Genealogical graph of the grape phylloxera in California. *A*, hibernant radicicole; *B–G*, successive radicicole generations; *H*, winged sexuparous migrant; *I*, sexes; *Z*, emergence above ground of the wandering radicicole larvæ.

abundance of resistant types of vines, types many of which normally bear galls in other localities. The result is that the California cycle (fig. 5) is purely parthenogenetic and is therefore greatly modified from the original cycle (fig. 4) occurring on wild vines, the natural hosts of the insect.

RÉSUMÉ OF LIFE HISTORY IN CALIFORNIA.

A résumé of the life history will be presented before all the different stages and habits of the phylloxera in California are discussed in detail. This résumé is confined to the biology of the insect on viniferæ and does not consider the life history on resistant roots.

Over 99 per cent of the phylloxeræ pass the winter as small brownish unmolted larvæ, the remainder hibernating after having passed one or two molts. All parts of the root system are used for hibernating quarters, but the majority cluster on the larger roots, following an upward migration in the fall.

Coincident with the first sap flow in early spring is the growth of the hibernants, but in a given vineyard the earliest individuals commence to grow fully six weeks before the most tardy ones, so that after the foliage has opened, hibernating larvæ are still to be found on the roots. The development of the hibernants is considerably slower than that of the summer broods, and the former mature on the average about five and one-half weeks after they commence their spring growth. The development of the larvæ is at all times influenced by the quality of food and by conditions of humidity and temperature.

Upon casting its fourth skin, the hibernant is mature and commences egg deposition. Its progeny are the first-generation phylloxeræ, and these on hatching from the eggs either settle beside the eggshell or go in search of new food. Many aphids settle on young growing rootlets and produce the fleshy swellings, termed "nodosities." Others settle upon older roots and produce swellings, termed "tuberosities." Still others develop on roots without causing the development of either perceptible swellings or lesions. Individuals feeding upon nodosities develop more rapidly than do those on the unswollen surface of the root. The nodosities usually decay within a few weeks after their formation, and in most cases the destruction of the rootlets follows. The tuberosities also usually decay in time. The rotting of the nodosities is not very serious, as the vine can supply new apical growth, but the decay of the tuberosities leads to the decay of the larger roots either wholly or in part, and as a result the vitality of the vine is greatly impaired, or the vine is killed outright.

The first-generation individuals are mature in from four to seven weeks after the eggs have been deposited, and they in their turn deposit eggs, which produce further generations throughout the summer and autumn.

Owing to the fact that, under favorable conditions, the adults deposit eggs during an average period of 45 days, an overlapping of generations ensues during the summer and fall. In order to avoid

confusion, it is assumed that there are five generations annually, since this number is about the average in a vineyard in which the sap moves early, although there might be, under certain conditions, from one to eight or even nine generations within a single year. The hibernant generation having matured in April, the succeeding generation matures about the time the canes have ended their first rapid growth, approximately the end of May. Succeeding generations mature on about the following average dates: Second, July 6; third, August 15; fourth, September 30; the fifth generation hibernating.

A variable percentage of the larvæ of generations 2, 3, and 4 becomes nymphs, and these later emerge from the ground as winged insects and either fly away or are borne off on the wind. Large numbers of these are caught in spider webs. Many of the newly hatched larvæ develop a wandering tendency just after they have issued from the eggshell and seek to emigrate to other vines either through the soil or over the surface of the ground. Large numbers of these migrating larvæ are also caught in spider webs on the surface, and while only a small percentage reach their destination, a single individual may start a new infestation. Those of the larvæ that succeed in fastening upon a root or rootlet develop as radicicoles. The winged forms normally occur from June to October, and the wandering larvæ are found from July to September.

During July and August, when the adult radicicoles are most prolific, incubation and development proceed most rapidly, and the phylloxera may be said then to have reached its most active stage. It is at this stage that the greatest damage is done to the roots of the vines, although the effects are not generally apparent until the fall and winter following, when the lesions formed during the summer have decayed.

At the end of September a few of the newly hatched larvæ hibernate, and throughout October successive generations become hibernants, so that by the end of the month a large majority of the phylloxera have reached this stage. During November and the first half of December, a few mature radicicoles and growing larvæ may be found, but after the middle of December, it is unusual to find any form but the hibernating larva.

Under conditions of abundant food supply, the period of egg deposition of the radicicoles averages 45 days and may reach a maximum of 110 days. This average is nearly constant throughout the season. The average number of eggs deposited is about 117, but under certain conditions the number may be increased to 486. The daily average number is about $2\frac{1}{2}+$ eggs, and as many as 23 eggs have been deposited in 24 hours by a single phylloxera.

The rate of egg deposition is usually indicated by a sharp rise shortly after commencement, followed by a gradual decline. During the period of egg laying the adult feeds, and after the last egg is laid may live for as long as three weeks.

Incubation naturally is influenced by temperature, and the duration of the incubation period may vary from five days in July to over a month in December. Very few eggs are laid in December, but in March and April, when many eggs are deposited, the maximum period of incubation is 27 days.

The larvæ mature in midsummer in about 15 days, and in April and November in about 34 days, and the hibernant generation develops in about 180 days. The winged forms mature more slowly than do the wingless individuals, since the fourth or nymphal instar is noticeably extended beyond that of the corresponding wingless stage.

In the late fall a few individuals intermediate in structure between the nymphs and radicicoles are found. These are called "nymphicals" or intermediates and, so far as is known, they deposit the same type of eggs as the radicicoles, although they are not prolific. From egg deposition to the molting of the final skin, the period covered by the sexes, which develop from eggs of two sizes laid by the winged forms, was about 12 days in confinement.

All stages of the phylloxera molt four times, and the first instar is always the longest (the adult instar excepted).

HIBERNATION.

The phenomenon of hibernation.—Throughout autumn and early winter an ever-increasing percentage of newly hatched radicicole larvæ, instead of increasing in size and maturing normally, remain as very small brown phylloxeræ (Pl. IX, *d*, p. 64). As winter progresses, the mature individuals die, leaving only the small brown larvæ and a few unhatched eggs. As soon as these late eggs hatch, the larvæ settle down, becoming brown like the others. These small larvæ are the hibernants, and as such they remain throughout the dormant period. Occasionally phylloxeræ that have passed one or two molts hibernate. This type is quite unusual, and probably consists of individuals that have reached a certain stage of development and are unable, through lack of nourishment, to mature, most of them dying before spring.

Hibernant larvæ occur on all kinds of vines—on viniferæ and on American varieties and hybrids. While this form of phylloxera occurs more or less sparingly on American resistant vines (*Vitis riparia*, *V. rupestris*, *V. berlandieri*, etc.) and on some American

nonresistant × resistant hybrids, it finds its greatest development on viniferæ and on certain American nonresistant varieties of *Vitis labrusca*, *V. aestivalis*, and *V. monticola*. On the wild species of Vitis of the eastern and southern parts of North America, considered as the original hosts of the grape phylloxera, is found a complicated life cycle embracing gallicoles (gall lice), radicicoles (root lice), winged migrants, sexed forms, winter eggs, and true stem mothers. The hibernants are rarely abundant on these wild species of vines, and the winter is passed chiefly in the winter-egg stage. On vinifera (*Vitis vinifera*) this complicated life cycle is rarely completed, and a simpler one, comprising only the root forms, obtains. Therefore, in the absence of the winter egg, the winter period must be tided over by another form, which is supplied in the hibernant larva. It appears that, to the phylloxera, *Vitis vinifera* is an acquired food plant, and that the nature and construction of the Old World grapevine has changed the habits and life history of the grape phylloxera feeding on it.

On viniferæ, although hibernation takes place chiefly on the larger roots and on the subterranean portion of the trunk, it occurs also on nodosities and on smaller roots.

Hibernants are located both on lesions and on the normal surface of the roots. On the varieties of resistant vines and certain hybrids (vinifera × resistant and resistant × American nonresistant) that have been examined, it has been found that hibernation occurs chiefly on nodosities and less frequently on the normal root surface. Tuberosities rarely are formed on these vines. On American nonresistant and vinifera × nonresistant hybrids, hibernation was chiefly of the type found on the viniferæ. On Golden Champion, Agawam, Catawba, Isabella, Lenoir, and Delaware, hibernants occurred on tuberosities, nodosities, and the normal root surface. On Moore's Early they were located on nodosities and on larger roots but not on tuberosities.

Appearance of hibernants.—The hibernants (Pl. IX, *d*, *e*, *f*, p. 64) appear as little oval brown insects flatly appressed to the surface of the root, their legs folded underneath the body. The antennæ are borne at right angles to the major body axis, and hardly project beyond the maximum width of the body. The whole insect generally shows one color, but sometimes there is a darker median longitudinal line, except on the head. In those individuals which have molted before going into hibernation, a similar shade of darker brown occurs. Occasionally lighter individuals will be noted, but none is ever as pale as the growing and feeding radicicole larvæ. Hibernants located under several layers of bark, as a rule, exhibit a paler color than those living more exposed.

FIXATION OF BEAK.

To secure information regarding the fixation of the beak in the root five lots of hibernants were examined on January 23, 1914. The results are given below.

TABLE II.—*Fixation of beak of hibernants of the grape phylloxera.*

Lot No.	Number of individuals.	Number with beaks fixed.	Number with beaks free.	Remarks.
1	25	12	13	Under 2 layers of bark on large root.
2	25	24	1	Large root; insects originally under 2 layers of bark, but layers peeled off some time before experiment.
3	25	16	9	Small root; insects on tuberosities.
4	25	22	3	Do.
5	20	8	12	Under several layers of bark on stock of vine 3 inches below soil surface.
Total	120	82	38	

In lots 1, 2, and 5 the individuals that had their beaks fixed in the roots were obviously the more healthy. In lots 3 and 4 all the phylloxeræ appeared equally healthy. They were on more succulent roots than those in lots 1, 2, and 5, and it may be that on such succulent food the hibernants have a habit of driving in and drawing out their beaks at will, whereas on harder roots this would not be possible. It is evident that hibernants situated on the outside bark of a root are likely to be washed off by water if their beaks are not inserted into the root. The experiment would serve to indicate that in the individuals of lots 1 and 5, wherein the hibernants were protected under layers of bark, the majority had their beaks free, while in lots 2, 3, and 4, wherein the hibernants were exposed, the majority had their beaks inserted, so that it appears that the fixation of the beak acts as an anchorage.

NOURISHMENT.

The hibernant larva partakes of nourishment very slightly, if at all, before it settles for the winter. During the period of true hibernation it apparently takes no nourishment. Therefore it is probable that the great majority of the hibernants take their first food when they arouse themselves from their lethargy in spring. Of those observed to feed before hibernating, a few pass one or rarely two molts, while the rest remain unmolted but larger in size than the true hibernating larva. The writers have observed instances in which severed pieces of roots infested by hibernants formed winter lesions, the presence of the beaks in the root affording a stimulus.

Hibernants on nodosities sometimes keep these fresh until spring by the stimulating action of their implanted beaks. Such nodosities, especially in vinifera and labrusca vines, otherwise usually fail to pass the winter in a fresh condition, as they are susceptible to rot through moisture.

DURATION OF INSTAR.

With the exception of the winter egg, the hibernant instar is the longest found in the life cycle of the phylloxera. A series of experiments undertaken in the laboratory during the winter 1911–12 showed that the average for 12 individuals was 183 days, or approximately half a year. A later series of experiments, which took place both on living vines and in the cellar on severed roots, indicated that this period may be shortened to four and one-half months and lengthened to seven and one-half months, dependent, as usual, on food, temperature, and moisture conditions, and that six months is about the average period for the development of the hibernants. This period was considered from the date in the fall on which the insect hatched from the egg to that on which the insect became mature the spring following. The actual state of dormancy is from three to six weeks shorter, and thus approximates five months. Granted that radicicoles may live for three months after reaching maturity, it is apparent that hibernating phylloxeræ might attain a total longevity of over 10 months.

MOVEMENT ON THE ROOTS.

On a sound root, the overwintered phylloxeræ rarely change their positions while they develop. If situated on tuberosities or nodosities, they cause these lesions to become enlarged, and if situated on the normal root surface they cause the formation of new lesions. Occasionally they develop without causing a lesion to appear. On decayed and decaying roots, they move away after the first or later molts and seek better food. This movement is both upward and downward, indiscriminately, and is never extensive. The individuals show only feeble inclination toward migration. This generation appears to be the lowest in vitality and the quickest to succumb to adverse conditions.

GROWTH AND MATURING OF THE HIBERNANTS.

During the true hibernation period the phylloxeræ apparently take no food, and if any be taken no increase in growth can be noted. Later a slow but appreciable growth may be observed, which indicates the termination of the true hibernation period. A growing

period, varying from one to six weeks, ensues, and after this the first molt occurs. In the course of from two to six weeks after the first molt three additional molts take place, and at the conclusion of the fourth molt the phylloxera is mature. This spring growth and development, as observed in the vineyard and in cages, is extended over a period of about three and a half months, and usually occurs during the period from February 15 to April 15. The commencement of growth in phylloxera is noted to be coincident with the first movement of sap in the vine, and naturally both are influenced by prevailing meteorological conditions. Upon reaching the adult stage the hibernant immediately begins the deposition of its eggs, and in this manner the series of parthenogenetic generations destined to continue through the season is commenced.

Measurements.—During the winter of 1913–14 hibernated larvæ were measured at certain intervals to determine at what time the spring growth started. On October 27, 1913, seven individuals which had recently hibernated averaged 0.333 mm. in length and 0.202 mm. in maximum width; on January 6, 1914, four individuals which had hibernated in October, 1913, averaged 0.337 mm. in length and 0.198 mm. in maximum width; on February 23, 1914, four individuals averaged 0.410 mm. in length and 0.217 mm. in maximum width; and on March 10, 1914, five individuals averaged 0.421 mm. and 0.241 mm., respectively. Between October and January there was no difference in size, but between January 6 and February 23 there was a marked difference, both individually and collectively, showing that between these dates the hibernants had begun to feed. The measurements of the individuals taken on March 10 showed that considerable growth occurred between February 23 and that date. None of the insects measured had molted, and observations showed that perceptible growth did not begin before February 10. The average length of the beak of the newly hatched radicicole destined to hibernate is slightly over 0.2 mm., but after it has been inserted in the root it becomes somewhat telescoped and measures about 0.17 mm.

The majority of the hibernants before they start to grow are smaller than the newly hatched radicicoles, and therefore they actually shrink in size after they hatch from the egg and settle to hibernate. Those that feed before hibernating do not shrink to such a small size.

Hibernation in vineyards.—In the vineyards it has been observed that the phylloxeræ enter into hibernation as early as September 15 and as late as December 15. Prior to October 1 only a small percentage of hibernants have been found, and after November 20

only a small percentage have been observed that were not hibernants. The greater number of the aphids enter hibernation during October and the first half of November; that is, a majority of the larvæ hatching from eggs in this period settle down to hibernate. A few of those hatching before October become hibernants. After December 1 it is very unusual to find eggs. The phylloxeræ do not enter into hibernation all at one time, and even on a single given grapevine the entering into hibernation is protracted over several weeks and often as long as two months. The causes that induce the young larvæ to hibernate instead of proceeding with their normal growth are three: (1) Condition of sap flow, (2) condition of food, (3) temperature and humidity. Hibernation in general takes place at the time when aerial and radical growth of the vine slacken in the fall. If the soil temperature is high, there is a tendency to postpone hibernating until some time after the terminal growths have apparently ceased. On decayed and decaying roots the phylloxeræ hibernate earlier and on nodosities and sound tuberosities later than on the surface of a normal root. Regarding the influence of temperature, Mayet (15), in discussing the hibernant form, states that eggs die when the temperature falls below 10° C. He states further:

> This temperature of 10° C. appears to be the minimum under which the insects become numb, and above which they go out of their torpor * * * M. Maurice Girard proved, experimentally, by means of a freezing mixture, that the phylloxera would sustain a temperature of —8° and —10° C. without dying.

The present writers' observations in the vineyards show that, broadly speaking, when the temperature drops to a minimum of 66° F. about half the individuals are hibernants, and when the maximum in spring has risen to 58° F. about half the individuals have commenced growing. The phylloxeræ enter hibernation under a considerably higher temperature than that which obtains at the time their spring growth begins.

Character of soil has no direct influence on hibernation, but it may have an indirect influence in so far as it may affect the condition of the roots. The heavier soils hold the moisture longer than those of lighter types, bringing about a more rapid decay of the roots and compelling early hibernation. Cold soils also force the insects into early hibernation.

In the vineyards the bulk of the hibernants occur on the lower part of the stump and on the basal portions of the main roots. Hibernants also ascend older vines several inches above the soil surface, where they are concealed under layers of bark. Often most of those that go above the soil surface perish from cold (16). On the smaller rootlets are found small numbers of hibernants, many of them on nodosities on which they pass the winter, frequently with a considerable percentage of mortality. On vines that have been heavily

attacked for years previous, it is unusual to find hibernants, except at the base of large roots or on the trunk, because the roots that were attacked the previous summer tend to rot badly when moistened by winter rains, and consequently most of the hibernants remaining thereon die, and only those higher up on sounder pieces of roots survive in abundance. The basal part of a large root is not generally badly attacked during summer, and so there are not enough tuberosities to rot it during the succeeding winter.

A very noticeable tendency is for the hibernants to congregate in masses. Such masses occur on the normal surface of the root, on tuberosities, on nodosities, and under one or more layers of bark. Perhaps in general on a grossly infested vine more masses occur on the outside bark, but this is only because the preferred sheltered places are too few and are inadequate to cover all the phylloxeræ. On younger vines a favorable location for hibernating is at the foot of the stump. On older vines this position is not so generally chosen. On vines which are only lightly infested the phylloxeræ often congregate at certain spots, while other spots, apparently as favorable, are neglected. On the heavily infested vines all the favorable spots for hibernation are utilized, the majority of the insects being forced to locate on the unsheltered outside bark of the root.

In vineyards the growth and maturing of the hibernants in spring extends over a period about as long as that covered by the entering into hibernation in the fall. The growth first becomes apparent about February 25, and proceeds until the time arrives when the most tardy individuals mature. Immature hibernants are found as late as May, but by April 15 the great majority have become mature. Just as in the case of "entering hibernation," so in the "spring development," a wide range occurs even on single given vines. The earliest individual may commence growth two months or more before the most tardy. On an average, it takes about five weeks for the hibernants to mature after they have first shown perceptible growth. On sound lesions this is shortened to as much as three weeks, and on decaying portions of roots lengthened to as much as eight weeks. Many of those on decayed roots die from ill nourishment before maturing, but the majority of such move away to seek better food.

The forces which influence the growth of the phylloxeræ in spring are a reversal of those which impel hibernation in the fall. As stated, the phylloxeræ start to grow about the time when the sap begins to flow. On dying vines in which the sap flow is either not apparent or very weak, the phylloxeræ on the more healthy roots show perceptible growth in like manner to those living on healthy vines, in which case their activity is supposedly due solely or chiefly to meteorological effect. The spring growth on unhealthy roots

is curtailed and commences late. On nodosities and tuberosities which have remained fresh during winter, the succulent condition of the food induces early growth on the part of the phylloxeræ.

Hibernation under cellar conditions.—During the period 1911–1915 hibernation was observed on severed roots in the laboratory cellar. These roots were kept in glass battery jars and in petri dishes and remained in a fresh condition when systematically moistened. Good callus growth and sometimes fleshy offshoots were obtained, especially when a layer of moist sand was placed in the bottom of the dishes. The phylloxeræ caused the formation of lesions in similar manner as on roots of living vines.

Under cellar conditions hibernation was often prolonged beyond the period found to occur in the vineyards, and this prolongation resulted in a small number of phylloxeræ maturing very late. The "awakening" period in spring was not different from that found in the vineyards under equalized temperatures. Under cellar conditions a greater mortality existed among hibernants than in the vineyards. This was supposedly due to the greater range of daily temperatures, to the abnormal condition of the roots severed from the vine, and to the apparent lack of sap flow. In the cellar hibernants a greater variation in size and color existed, even in unmolted phylloxeræ, than in the vineyard on living vines. A very small percentage of hibernants were observed to pass the winter in the second and third instars. Eggs were never observed to pass the winter, since all eggs laid late in the year hatched in due course according to temperatures. No mature or fourth-instar phylloxeræ were observed to hibernate. Adult radicicoles in late autumn, as at other times, lived for some days or even weeks after they deposited their last egg, but none was found that survived until spring.

Observations on the hibernation of phylloxeræ reared on severed roots under cellar conditions may be summed up as follows: The first phylloxeræ entered hibernation as early as August, in extreme cases in July, and the percentage of hibernating individuals from that time gradually increased. By October 1, it was found that on the average about 30 per cent of the individuals were hibernants. By the last of October from 85 to 90 per cent were hibernants. All the living phylloxeræ, however, were not hibernants until the end of December, and during November and December a dwindling number of adults and unhatched eggs were observed. All larvæ hatching after November 1 settled down to hibernate, and about three-fourths of those which hatched in October did likewise, the individuals comprising the other fourth maturing toward the end of October and in November and continuing to deposit eggs up to December.

The spring growth began in the earliest individuals about January 25; by the middle of March nearly all the phylloxeræ were growing and about half were mature. Some individuals remained dormant as late as the middle of April, and the most tardy did not mature until the middle of May or even later. On very poor roots many never matured at all. The period of appreciable growth prior to the shedding of the first skin averaged two weeks and the period from first molt to maturity about three weeks. On vigorous roots the hibernants mostly developed without changing their positions, but they forsook in large numbers roots decayed or decaying. These emigrations occur both before and after molting but chiefly just following a molt.

In comparing the hibernation on severed roots as observed under cellar conditions with that on living roots as observed in the vineyards, in pots, and in special box cages, several points are to be noted. (1) The phylloxeræ on the severed roots in the cellar entered hibernation in a more irregular manner than did those on the living vines. This condition appears due to the following causes: The severed roots were cut off from a normal flow of sap, the temperature fluctuations in the cellar were greater, and in the months of July, August, and September the temperature reached a lower daily minimum than in the vineyards; (2) the phylloxeræ hibernating in the cellar matured earlier in the spring than those on living vines out of doors by reason of the higher temperature obtaining in the cellar during January and February; (3) there was a greater mortality among the hibernants in the cellar, due to the fact that the severed roots often dried up or decayed before spring; (4) numbers of the phylloxeræ occasionally hibernated after they had shown appreciable growth or even cast a skin. This phenomenon rarely has been observed on living roots. In other respects the behavior of the phylloxeræ on severed roots did not differ from that on living roots. In exceptional cases vigorous pieces of severed roots were observed to send out fleshy rootlets in early spring, indicating a modified sap flow, and on such roots the phylloxeræ moved early and appeared to be influenced by this flow of sap. The comparatively high winter temperatures obtaining in the cellar undoubtedly produced this modified sap flow, since it occurred much earlier than the corresponding flow in the vineyards.

Hibernation on vinifera vines in cages, 1913–14.—The following observations were conducted upon the roots of living vines of different varieties growing in special cages (Pls. V–VII, p. 52). The vines were young and satisfactory specimens for the experiments. The exposed portions of the roots between the upper and lower pots were about 4 inches long, one-fourth inch in diameter, and from 10 to 14 inches below the soil surface of the upper pot. Although both ends

of the exposed portions of roots were surrounded by an inch of fine sand, and all inoculations were made on these exposed portions, it frequently happened that phylloxeræ found their way to the unexposed portions, so that in the winter following the inoculations hibernants were found in both the exposed and unexposed portions.

The temperatures in the cages differed but slightly from those recorded simultaneously 2 feet below the soil surface in the laboratory vineyard. In 1913–14 in midwinter, however, the former touched a mark about 10° F. lower, besides being uniformly lower throughout December and January in both the seasons 1913–14 and 1914–15. During the period (August to November) in which the phylloxeræ entered hibernation there was no appreciable difference, and before the commencement of the spring growth of the hibernants the temperatures were again equalized. Thus, in the periods of entering into and awakening from hibernation, vineyard conditions were reproduced in the cages as far as temperature was concerned. Contemporaneous vineyard observations show that the behavior of the hibernants on living vines in the cages simulated closely the behavior of those in the vineyards in the locality, and the habit of clustering was often noted. The aphids entered into hibernation and showed spring activity much as they did in the vineyards, but in each phenomenon there was an exception. In 1914, six aphids out of a lot of nine individuals hatching between August 24 and 26 proceeded to hibernate. Such early hibernation with succulent food present is quite unusual in the field. Again, in 1914, on another vine, part of a series of hibernants cast their skins as early as February 23, indicating that growth commenced not later than February 15. In the vineyard, even upon warm soils, the first date of activity was never earlier than February 25. This early spring activity in the cages was possibly due to comparatively high temperatures in February, this being the only month during which the cage temperatures exceeded those in the soil.

Hibernation on American resistant and nonresistant vines in cages, 1914–15.—Along with the vinifera vines planted in the special cages for observing the phylloxeræ on living roots, a number of American resistant and nonresistant vines were used for similar observation. The nonresistant varieties (propagated from *Vitis labrusca* and *V. aestivalis*) were Catawba, Isabella, Lenoir, Delaware, and Champion. The Muscadine (*V. rotundifolia*) was used also. The resistant hybrids, some of which were grafted to viniferæ, comprised Mourvedre × Rupestris 1202, Solonis × Riparia 1616, Berlandieri × Riparia 157.11, Riparia × Rupestris × Aestivalis × Monticola 554.5, Aramon Rupestris Ganzin 1, Riparia Gloire de Montpelier, Rupestris St. George. These vines were planted in the spring of 1914 and inoculated thereafter.

On the Muscadine the phylloxeræ upon hatching from the eggs refused to settle or feed. The nonresistant varieties were infested throughout summer and autumn, and on their roots the phylloxeræ entered into hibernation from September 20 to the beginning of November; in the case of the Champion, they hibernated as late as December 1. On the Catawba and Champion, the most heavily infested, the aphids began hibernation earlier; on the less infested Delaware, Isabella, and Lenoir, somewhat later.

Aphids became active about the middle of February, and all hibernants were adult by April 13. This spring activity was somewhat in advance of that occurring in vineyards, but was similar to that which occurred on the caged vinifera vines. On all nonresistant varieties it was observed that the hibernants massed on tuberosities, nodosities, and the normal surface of the roots; and in cracks in a manner similar to that observed to occur on vinifera vines.

On the resistant hybrids repeated inoculations during summer and autumn failed to produce more than an extremely light infestation. The phylloxeræ settled to hibernate during October, and at the end of that month all were hibernants. They were situated on side rootlets and on the normal surface of the root, but on the Rupestris St. George hibernants occurred also on nodosities which they had caused to form shortly after they settled.

Hibernation on American vines in pots, 1912–1915.—A large series of 2-year-old vines (from cuttings) planted in 6-inch pots, originally used in resistance experiments and comprising resistant vines, were examined during the years 1912 and 1913 for hibernant observations. It was found that hibernation took place during the last half of October and first half of November and that the spring awakening proceeded from about March 10 to April 15. These vines were planted in light sandy soil. The hibernants settled chiefly on nodosities and to a smaller extent on the surface of the larger rootlets. In the spring there was a great variation in the growth of the vines. In the majority of instances the phylloxeræ on the early leafing vines molted sooner than those on the more backward plants. No temperature records were kept with this series, but it is probable that the records taken 2 feet below the soil surface (Table XII) approximated that which occurred in the pots in the winter of 1913–14.

A further series (1914) of rooted vines in 9-inch pots, comprising Agawam, Isabella, Lenoir, Delaware, Catawba, and Champion, showed that with the exception of the Delaware, which was lightly infested, hibernation proceeded from about October 1 to November 1, nearly all the insects being hibernants on the latter date. On the Delaware none of the phylloxeræ were hibernants on October 30, and the roots were on that date still running strongly in sap, while the sap flow in the other varieties was weaker. The temperature in

these pots was about the same as that occurring 2 feet below the soil surface. In the spring of 1915, on the Champion, Lenoir, Catawba, and Isabella, the phylloxeræ began to grow about March 1. On the first three the bulk of the hibernants were mature April 6, but on the Isabella, which was moribund, more than half were unmolted. This vine was not retained further, but, considering the condition of its roots, it is not probable that any of the phylloxeræ would have matured. The vine was too weak to send out new rootlets, and the roots showed much decay. The abundance of phylloxeræ the summer previous had doubtless caused this weakness.

THE RADICICOLE.

EGG DEPOSITION.

The adult radicicole commences to deposit eggs within 48 hours after the final molt. Occasionally there occur abnormal individuals which delay deposition of eggs as much as two weeks, and again there are others which fail to deposit eggs but continue alive for some weeks.

Egg deposition on severed roots.—Table III gives the summarized record of the egg deposition of radicicoles under cellar conditions during the years 1911–12.

TABLE III.—*Summarized record of egg deposition of radicicoles of the grape phylloxera under cellar conditions during 1911–12, Walnut Creek, Calif.*

Generation.	Number of adults.	Egg-laying period for generation.	Number of eggs per adult.			Days in period of deposition.			Average number of eggs per adult per day.
			Maximum.	Minimum.	Average.	Maximum.	Minimum.	Average.	
[1] 0	52	Apr. 21 to Oct. 1	347	4	84.6	110	2	55.3	1.53
1	45	May 27 to Sept. 23	486	10	192.0	96	5	46.3	4.1
2	57	June 29 to Nov. 6	287	2	102.0	106	1	48.5	2.1
3	17	Aug. 4 to Dec. 7	266	3	141.8	96	2	44	3.2
4	[2] 11	Sept. 5 to May 15, 1912	119	31	67.2	83	23	41.7	1.6
[3] 5–10	27	Apr. 26 to Oct. 6	137	4	35.5	47	3	21.5	1.7

[1] Overwintered generation. [2] Including 3 individuals which matured in 1912. [3] Throughout 1912.

Neglecting the series of generations 5 to 10, the individuals of which suffered through abnormal food and other conditions, it is shown in Table III that the aphids of the second generation were the most prolific. One aphid deposited 486 eggs in 79 days, an average of 6.3 per diem. The greatest number of eggs laid within 24 hours by a single adult was 23 and the longest laying period covered 110 days. A true seasonal average of the number of eggs deposited by each aphid was 117 for 1911 and a similar average of the number of eggs per diem per aphid about $2\frac{1}{2}$.

In 1913, between June 26 and November 14, a series of observations on fecundity under adverse food conditions was made. Among a large number of aphids, on two occasions only were as many as six eggs deposited in one day by a single individual. In the cellar, 431 eggs were deposited in a total of 331 days (1.3 eggs per diem per aphid), and in an electric incubator, wherein a slightly higher temperature was maintained, 787 eggs were laid in a total of 463 days (1.7 eggs per diem per aphid). These averages were considerably less than corresponding ones found to result in the 1911 series, yet the insects raised in the incubator were subjected to higher temperatures than were those in 1911, raised in the cellar.

Egg deposition on living vines.—During the years 1913, 1914, and 1915, series of generations were raised on living vines in cages. These vines were all viniferæ, and comprised the following varieties: Muscat, Zinfandel, Mission, Burger, Thompson's Seedless, and Grenache. The principal object in this work was to check up on the previous 2-year study of root cuttings under cellar conditions. The initial inoculations in 1913 were made with eggs laid by adults of the overwintered generation on Zinfandel vines in the vineyard, and thus no record of the egg production of the overwintered adults was secured in the cages. Of the first generation, records of 10 individuals were taken, but a complete record of only one was made, and this adult, between June 25 and July 14 (20 days), deposited 121 eggs, the largest number in a single day being 12. The 10 adults deposited 482 eggs in 95 days, or an average of 3.1 eggs per diem per adult.

Most of the individuals died early, and it is assumed that if they had been allowed to lay their full complement of eggs, the period of decline would have reduced this average. These adults were produced, 7 on Burger roots and 3 on Mission roots. It appeared that those on the Mission were the more prolific. On both varieties some were situated on lesions they had caused to form. These averaged better in egg production than the others situated on the normal root surface. Records for 14 adults of the second generation were taken. On a very healthy Mission root, living on lesions, 4 adults averaged 4.5 eggs per adult per diem. On two less healthy Mission roots of the same cage vine, 6 averaged 2.4 eggs per adult per diem. On a very healthy Burger root 4 averaged 3.9. The longest egg-laying period for any adult of this generation was 26 days and the maximum eggs per day 15. In all, 489 eggs were laid in 136 days, 3.6 eggs per adult per diem.

The egg-laying period of this generation ran from July 8 to August 15, with an average temperature of 68° F. Four adults of the third generation deposited 284 eggs in 88 days, at an average of 3.2 eggs per diem per adult; the longest egg-laying period was 28 days and the maximum number of eggs per diem was 8. These

adults lived on a healthy Muscat root on tuberosities, their egg-laying period being from August 28 to September 26, under an average temperature of 64° F. One of them did not commence depositing eggs until the sixth day after it matured, having moved about considerably meanwhile. The fourth-generation phylloxeræ wintered on the same root upon which their immediate progenitors had oviposited and matured in the spring of 1914. Of these, 3 adults laid 79 eggs in 42 days (aggregated) or 1.9 eggs per diem per adult. The maximum number for one day for a single adult was 4 and the longest egg-laying period 24 days. In this period one adult laid 56 eggs. The egg-laying period, toward the end of which the root became lightly decayed, ran from April 6 to May 8, under a temperature averaging 58° F.

In the ensuing generations throughout 1914 and 1915, the egg-laying records were mostly incomplete. Records of the fifth generation on Muscat in the period May 28 to June 11 show an average number of eggs per diem per adult to be 2.8, the largest number deposited in a single day by a single adult being 5. The average temperature was 65° F. Records of the seventh generation on a slightly decayed Grenache root, July 29 to August 8, show an average number of eggs per diem per adult to be 5.4, and the maximum number of eggs laid in a single day to be 7. The temperature averaged 71° F. The records of these two lots are much too meager for comparisons.

In comparing the egg production on the living vines with that on root cuttings, it should be stated that during the summer and fall months the aphids on the former enjoyed higher temperatures. This advantage was somewhat counterbalanced by the greater daily fluctuations in temperature which took place on caged living vines and which frequently resulted in a daily minimum lower than that simultaneously occurring in the laboratory cellar in which the root cuttings were kept.

As a general rule the egg-depositing capacity of the adult increases rapidly after maturity, and after the zenith is reached decreases slowly, so that half the complement of eggs is deposited before one-third of the egg-laying period is completed.

The condition of the food is the chief factor in the production of eggs, but there is also a meteorological control. Frequent fluctuations in temperature and humidity adversely affect deposition.

Extrusion of the egg.—During the process of egg extrusion, which occupies from 20 to 40 minutes, the abdomen of the adult radicicole is considerably distended. It is apparent, therefore, that when an adult deposits 23 eggs within one day, extrusion will be taking place intermittently for a very considerable part of the day. During the

period of egg deposition, the aphids often change their orientation by pivoting about the beak.

Time of day of oviposition.—Between April 28 and May 25, 1913, records were taken in the cellar to obtain data upon the time of day of oviposition. The maximum daily temperature occurred about 6 p. m.,[9] and the minimum about 7.30 a. m. Between 9 a. m. and 5 p. m. (8 hours), 41 eggs were deposited, and between 5 p. m. and 9 a. m. (16 hours), 52 eggs were deposited in the 27 days. Between 9 a. m. and 5 p. m., there was an average hourly temperature in excess of that occurring between 5 p. m. and 9 a. m. of about 0.02° F. It is apparent that the higher temperature of the shorter period caused a comparatively greater number of eggs to be deposited, since the 52 eggs were laid in exactly double the time in which the 41 were deposited.

Egg fertility and mortality.—A large series of experiments took place in 1911 to determine the fertility and mortality percentages of the eggs of the radicicole phylloxera. These were carried on about evenly throughout the year. One series was conducted under cellar conditions in petri dishes, and the other took place in the laboratory under a higher temperature and was exposed to subdued daylight. Table IV gives the results of these experiments:

TABLE IV.—*Fertility and mortality of the radicicole egg of the grape phylloxera, Walnut Creek, Calif., 1911.*

Generation and environment.	Total number of eggs deposited.	Number of eggs hatched.	Number of eggs that failed to hatch.	Percentage hatched.
Unknown (various)	965	772	193	80.00
1 (Cellar)	1,000	911	89	91.10
1 (Exposed to light)	490	422	68	86.12
1 (Total)	1,490	1,333	157	89.52
2 (Cellar)	1,840	1,716	124	93.26
2 (Exposed to light)	245	236	9	96.33
2 (Total)	2,085	1,952	133	93.62
3 (Cellar)	1,112	987	125	88.76
4 (Exposed to light)	524	486	38	92.75
Grand total	6,176	5,530	646	89.54

There was no appreciable difference between the fertility of those reared in the cellar and of those reared in the higher temperatures of the laboratory rooms. The results indicate that on the average almost 9 eggs out of every 10 laid will hatch. It is probable that vineyard conditions produced similar averages as no predators or other causes that might bring about a different average have been observed with the exception of the case of excessive spring moisture acting upon the eggs laid by the overwintered adults and in the case

[9] All references to clock time refer to "Standard time."

of eggs laid on rotting tuberosities. The eggs have a considerable resistance to water at ordinary temperatures and may also hatch under water. Many, probably 25 per cent, of those that are laid on rotting tuberosities fail to hatch. They seem to be so impregnated with dampness and influenced by the rotting root tissues surrounding them that they turn dark brown prematurely and finally collapse after the embryo dies. It must be considered also that very slight pressure applied to the eggshell may rupture it and kill the embryo.

INCUBATION PERIOD.

The first incubation record at Walnut Creek took place during April, 1909. Between April 9 and April 26, 24 eggs were observed in the laboratory with the results shown in Table V:

TABLE V.—*Incubation period of the eggs of the grape phylloxera, Walnut Creek, Calif., 1909.*

	Days.
Average incubation stage	13.8
Maximum incubation stage	15
Minimum incubation stage	12

No temperature records were taken. The eggs were presumably deposited by overwintered adults. During 1911 and 1912 a large series of incubation records was obtained. Table VI gives incubation records for each generation during 1911.

TABLE VI.—*Incubation records of the eggs of the grape phylloxera at Walnut Creek, Calif., 1911.*

Generation.	Environment.	Dates of period of incubation.	Average temperature.	Number of eggs laid.	Incubation period.		
					Maximum.	Minimum.	Average.
					Days.	*Days.*	*Days.*
[1] I	Cellar	Apr. 28–May 18	61	49	17	10	13.6
[2] I	do	June 4–Aug. 19	64	889	15	8	10.8
[2] I	Laboratory shelf	June 13–Sept. 6	([3])	412	13	7	9.8
II	Cellar	June 13–Aug. 19	64.5	1,797	14	7	10.2
II	Laboratory shelf	June 5–Aug. 18	([3])	235	11	6	8.5
III	Cellar	July 7–Aug. 20	64.6	969	14	7	11.7
IV	Laboratory shelf	Aug. 9–Sept. 2	([3])	551	10	6	7.2
IV	Cellar	Aug. 18–Oct. 26	64	10	18	7	13.3

[1] Eggs deposited by overwintered adults.
[2] Later series of eggs deposited by overwintered adults.
[3] Temperature at least 5° higher than that in cellar at corresponding dates.

From Table VI it will be seen that the influence of temperature was very considerable. The records of 1912 are much more scanty and bear out the observations of 1911. Under an average temperature of 70° F. the egg stage in 1912 averaged 8.9 days, with a maximum and minimum of 10 and 7 days, respectively. The period covered was from June 19 to October 3, but the great majority of the total of 55 eggs were laid during June. A small series of 27 sixth-

generation eggs, laid May 6 to 8, 1912, under an average temperature of 63° F., incubated in an average of 10.7 days.

The results shown in Table VII were obtained during 1911 and are in part a complement of those shown in Table VI:

TABLE VII.—*Incubation records of the eggs of the grape phylloxera, Walnut Creek, Calif., 1911.*

Group No.	Environment.	Average temperature.	Month of incubation.	Number of eggs.	Egg stage.		
					Average.	Maximum.	Minimum.
		° F.					
1	Exposed to light	57	April	43	15.14	18	13
2	do	60	May	177	11.03	15	9
3	do	65	June	352	9.07	12	8
4	do	52	November	16	15.09	18	15
5	In darkness, laboratory drawer	62	May–June	323	10.66	14	9

The eggs of the first four groups in the preceding table were exposed to light on a shelf in the laboratory, and those of group 5 were incubated in a drawer in the laboratory. Both lots were subjected to a very abnormal fluctuation of temperature, this fluctuation in some cases reaching 20° F. daily.

In 1912, 1913, and 1915 some additional incubation records were obtained, and Table VIII indicates the relations between temperature, environment, and incubation to cover the four years, 1911, 1912, 1913, and 1915.

TABLE VIII.—*Relation between incubation, temperature, and environment in the egg deposition of the grape phylloxera, Walnut Creek, Calif., 1911–1913 and 1915.*

Lot No.	Year.	Number of eggs.	Average daily temperature.	Incubation.	Remarks on environment.
			° F.	*Days.*	
1	1911	16	52	15.09	Exposed to light.
2	1915	13	55	20.50	Cellar.
3	1913	26	56.6	[1] 19.60	Do.
4	1911	43	57	15.14	Exposed to light.
5	1915	17	59	15.50	Cellar.
6	1911	177	60	11.03	Exposed to light
7	1915	16	60.5	15.40	Cellar.
8	1911	49	61	13.60	Do.
9	1913	38	61.3	15.50	Do.
10	1912	26	63	10.70	Do.
11	1913	48	63	15.50	Do.
12	1915	28	63.8	11.00	Do.
13	1911	889	64	10.80	Do.
14	1911	10	64	13.30	Do.
15	1911	1,797	64.5	10.20	Do.
16	1911	969	64.6	11.70	Do.
17	1911	286	65	10.29	Laboratory drawer—darkness.
18	1911	352	65	9.07	Exposed to light.
19	1915	13	65	9.40	Cellar.
20	1913	20	67	9.65	Do.
21	1915	22	67.3	8.80	Do.
22	1913	22	68	9.00	Do.
23	1915	62	68	[2] 7.00	Do.
24	1915	21	68.5	7.60	Do.
25	1912	55	70	8.90	Incubator.
26	1913	61	70.3	8.40	Do.
27	1913	38	72	8.70	Do.

[1] Maximum, 27 days.

[2] Minimum, 5 days.

Examination of Table VIII shows that the incubation period gradually becomes shorter as the temperature rises.

The exposure to light apparently produced abnormal rapidity in the development of the eggs. In lot 18 this influence was scarcely felt, while in lots 1, 4, and 6 it was very cogent, and it is evident that exposure to light is chiefly influential under low temperatures. The comparatively slow development of lots 25 to 27 apparently can be laid only to temperature fluctuations obtaining in the incubator. This fluctuation in the incubator sometimes consisted in the maintenance of a lower minimum for a longer period than that which obtained in the main part of the cellar. Such temperatures possibly would exert a retarding effect upon egg development that would not appear in the averaged readings of the thermometer.

Even among the lots kept in the cellar under similar conditions there were apparent exceptions to the rule that "the higher the temperature the shorter the period of incubation." One such instance is that of lots 15 and 16, in which two large series were used, yet under temperatures differing but 0.1° F. there was a difference in the average incubation periods of one and a half days.

Among the individuals enumerated in Table VIII the maximum egg stage was 27 and the minimum 5 days. The respective average temperatures influencing the two individuals were 55° F. and 68° F., and both were incubated in the cellar. It was possible only to estimate an annual average incubation stage, and this was about 11 days. It should be added that eggs have been observed in December to incubate in a period exceeding 30 days, but it is unusual to find eggs at this time of year.

Experiments conducted in the cellar demonstrated that eggs incubated as rapidly in arid as in humid surroundings, but submergence in water lengthened the incubation period, even under equal temperatures.

Incubation on living roots.—During the years 1913, 1914, and 1915 biologic records were made on the living roots of young vines of viniferæ and vinifera × American hybrids. A series of generations were conducted during these three years, and incubation was observed for each generation. In most cases immediately after deposition the eggs were removed to an unifested root, but in some they were allowed to incubate where they had been deposited. The cages containing the experimental vines were all placed together in one trench, and the temperature was alike in all of them. Table IX indicates the incubation periods with reference to temperatures and time of year. The years are not given, as in some instances

single lots containing individuals incubating under the same average temperatures but belonging to more than one year have been combined.

TABLE IX.—*Incubation of the eggs of the grape phylloxera on living roots, Walnut Creek, Calif., 1913–1915.*

Lot number.	Number of eggs.	Average temperature.	Incubation.	Months or month.
		° *F.*	*Days.*	
1	19	56.8	[1] 19.0	March to April.
2	11	57	15.1	April.
3	11	58	14.8	April to May.
4	([2])	58.5	15.0	Do.
5	7	60	12.3	Do.
6	6	61.8	11.2	May to June.
7	([2])	62	9.0	Do.
8	28	63	9.0	Do.
9	([2])	64	9.7	June.
10	3	66	[3] 9.5	Do.
11	11	68	10.5	September to October.
12	23	69	[3] 8.2	June to October.
13	26	70.5	[3] 7.7	June to September.
14	21	71.5	9.4	Do.
15	11	72	8.4	August.
16	45	72.5	[3] 7.7	July to September.
17	23	73	[3] 7.0	Do.
18	8	73.2	[3] 6.4	July.

[1] Maximum, 20 days. [2] About 20. [3] Minimum, 6 days.

Many of the lots contained a very small number of individuals, but in the main the incubation stage became progressively shorter as the average temperature rose. Between the temperatures of 56.8° and 62° F. the incubation periods are rapidly reduced, while between 62° and 73.2° the reduction is much less rapid in proportion to the rise in temperature. This is a somewhat similar condition to that found in the cellar records.

It is evident that the stage was shortest during the months of July and August, and longest during the months of March and April. Records began as early in the year as March 31, and closed as late as October 5. Two of the individuals in lot 1 incubated in the maximum period of 20 days (Mar. 31 to Apr. 20) under an average temperature daily of 56.8° F. The minimum of six days was reached by 17 individuals in each of the months from June to September under average daily temperatures of from 66° to 73.2° F.

The condition of food had no apparent effect upon the duration of the egg stage. Eggs deposited by radicicoles which had developed from eggs deposited by gallicoles received from Virginia incubated in the same average period as those descended from radicicoles of many generations, and eggs deposited by nymphicals incubated precisely as did those laid by normal radicicoles. Individual incubation records, both of eggs reared in the laboratory cellar and of others reared on living vines, are given in connection with the development of the radicicoles under the same conditions in the section on "Development of the radicicole larva," pages 54, 55, 57, 60–62, and 63.

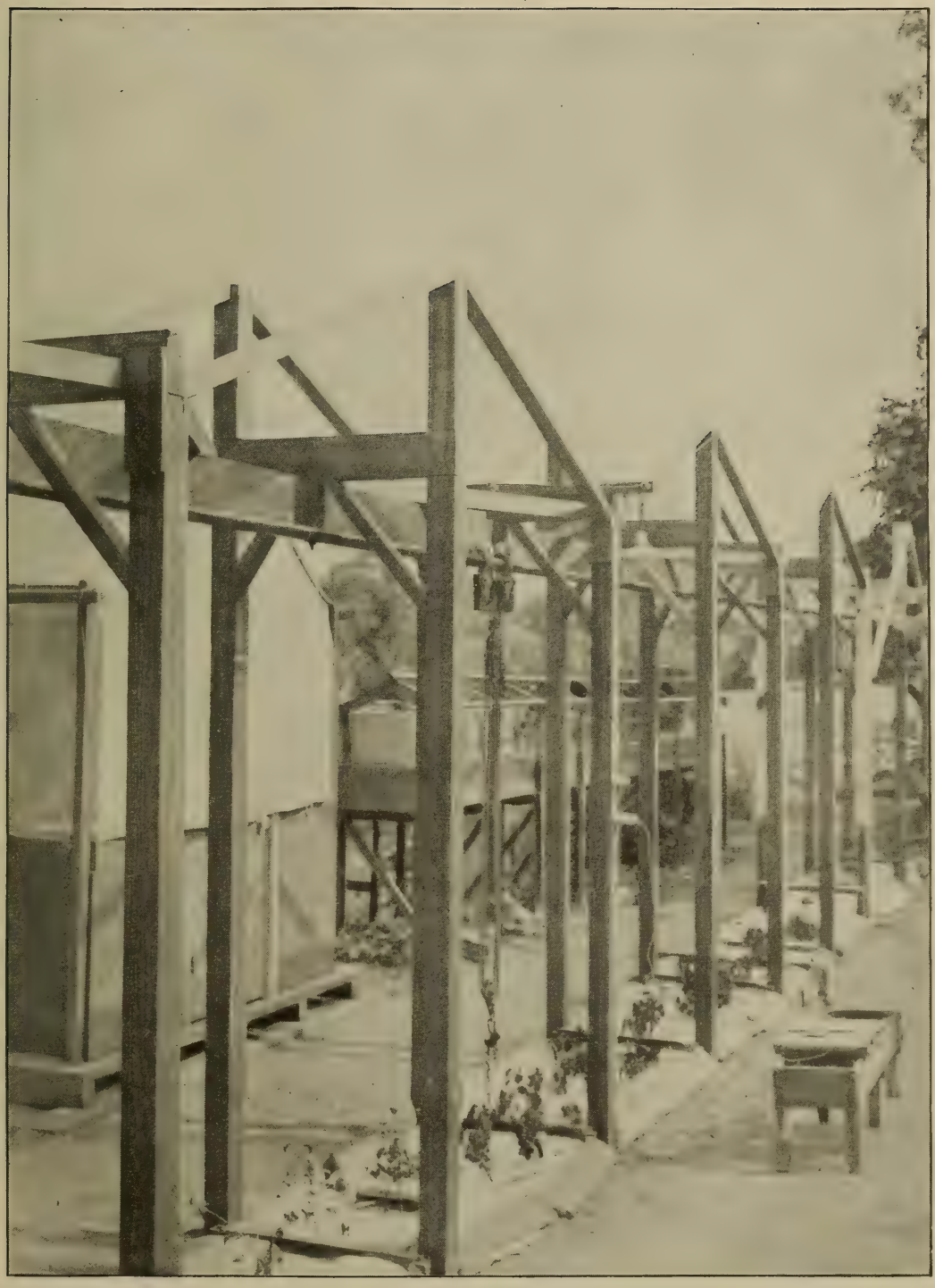
METHODS OF REARING THE RADICICOLE LARVÆ.

During 1911 and 1912 the radicicoles were reared exclusively, both within and without an electric incubator, in the cellar. The roots on which the phylloxeræ were reared were kept in glass jars and in petri dishes with moistened filter paper. This method was not always satisfactory, since it was not easy to maintain an even humidity similar to that existing under natural conditions.

In 1913, 1914, and 1915 the insects were reared in the cellar and in the cages described below. The jars in the cellar were moistened by a layer of wet sand placed in the bottom. This method was more successful than in the case where moistened paper was utilized; the roots did not decay or dry up so rapidly, and they remained in much better condition through the winter.

These cages (Pls. V; VI, fig. 1; VII), constructed to hold young vines, may be described as follows: A trench 3 feet deep was dug wide enough to hold the cages with a space about 1 inch wide on each side. To prevent air passing down the cracks, small blankets were laid across the spaces, and this resulted in a temperature inside the cages of scarcely greater fluctuation than normally occurred 2 feet underground. The cages themselves were made of paraffined pine with an extra redwood bottom, and had two compartments, one above the other (Pl. VII). The upper compartment had on each side one, and the lower two, detachable boards the whole length of the major sides, and these boards were detachable to permit examination of of the roots and the removal of the pots. The upper compartment contained one and sometimes two pots (8 or 9 inches in diameter), around the top of which was fitted the topmost board of the cage, the outside measurements of which were 22 by 13 by 27 inches. The lower compartment contained 9-inch pots in saucers.

The method of planting the vines in the pots of the cages was as follows: Into the middle board of the cages were fastened one or two saucers having holes bored through them. A short piece of glass tubing larger inside than the diameter of the roots was fixed into these holes with a cone of paraffin. Two half pots, bottomless, were bound together by wire or tin bands to make a single whole pot, and placed to rest on the saucer. The vine was then put in place, certain of its roots being passed through the holes in the saucer and protruding below. The upper pot was then filled with soil with a thin top layer of fine sand. In the lower compartment, whole 9-inch pots, one or two, as the case might be, were put in place in their saucers, and the protruding roots planted in them, at the surface of the soil passing through about 3 inches of glass cylinder. The surface of the soil in the lower pots was covered in most cases with a thin layer of fine sand. Fine sand was tamped into the glass cylinders,



THE GRAPE PHYLLOXERA IN CALIFORNIA.

General view of pit and rearing boxes employed in life-history studies of the grape Phylloxera.

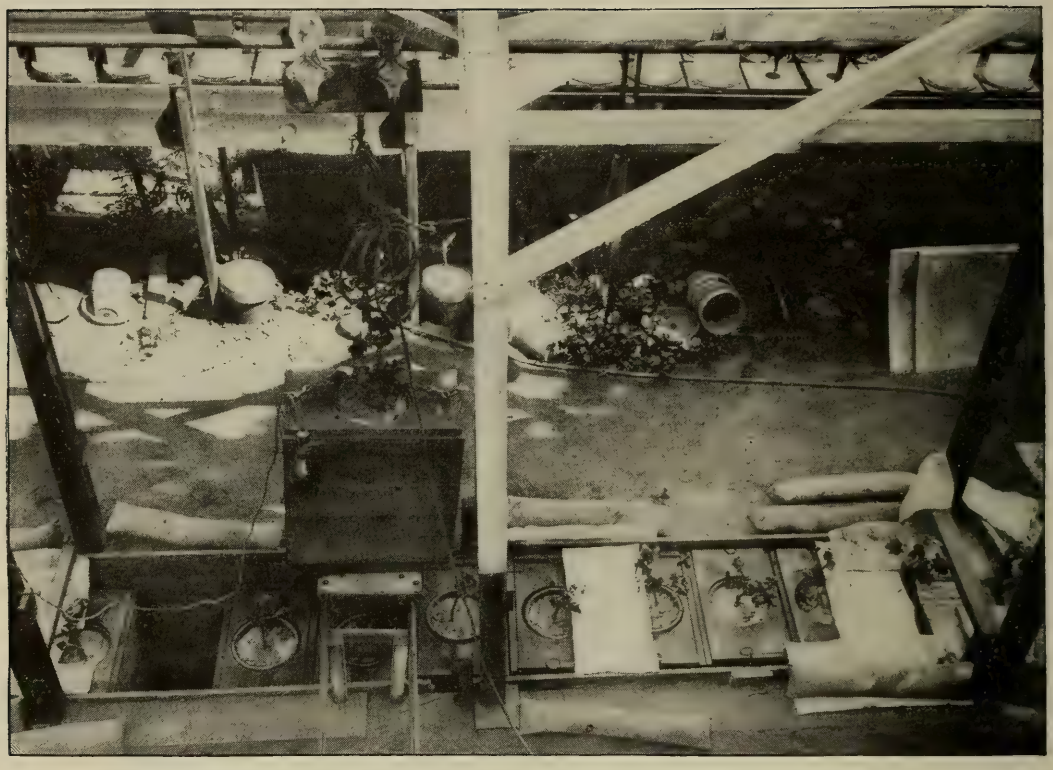


FIG. 1.—Pit with rearing boxes, illustrating method of covering with quilted strips to preserve same temperature as in like depth of soil.

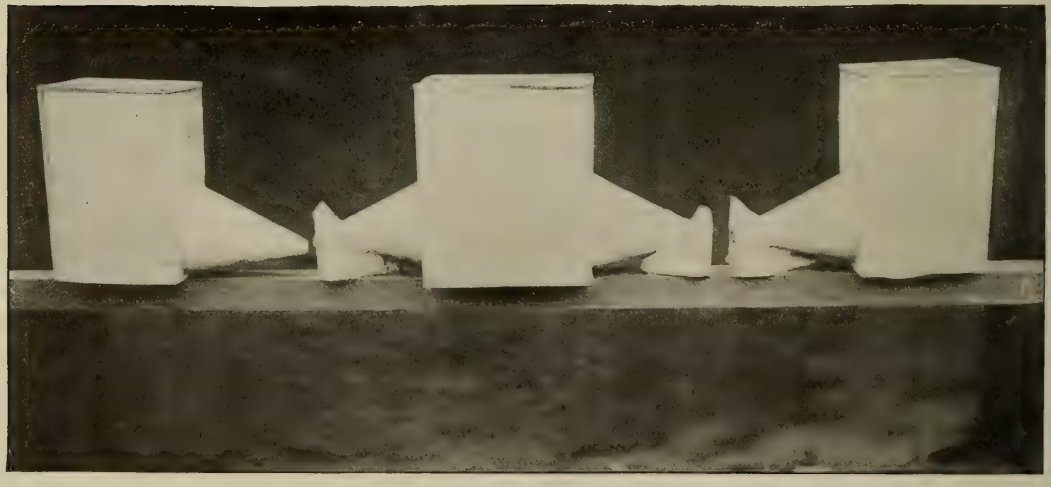
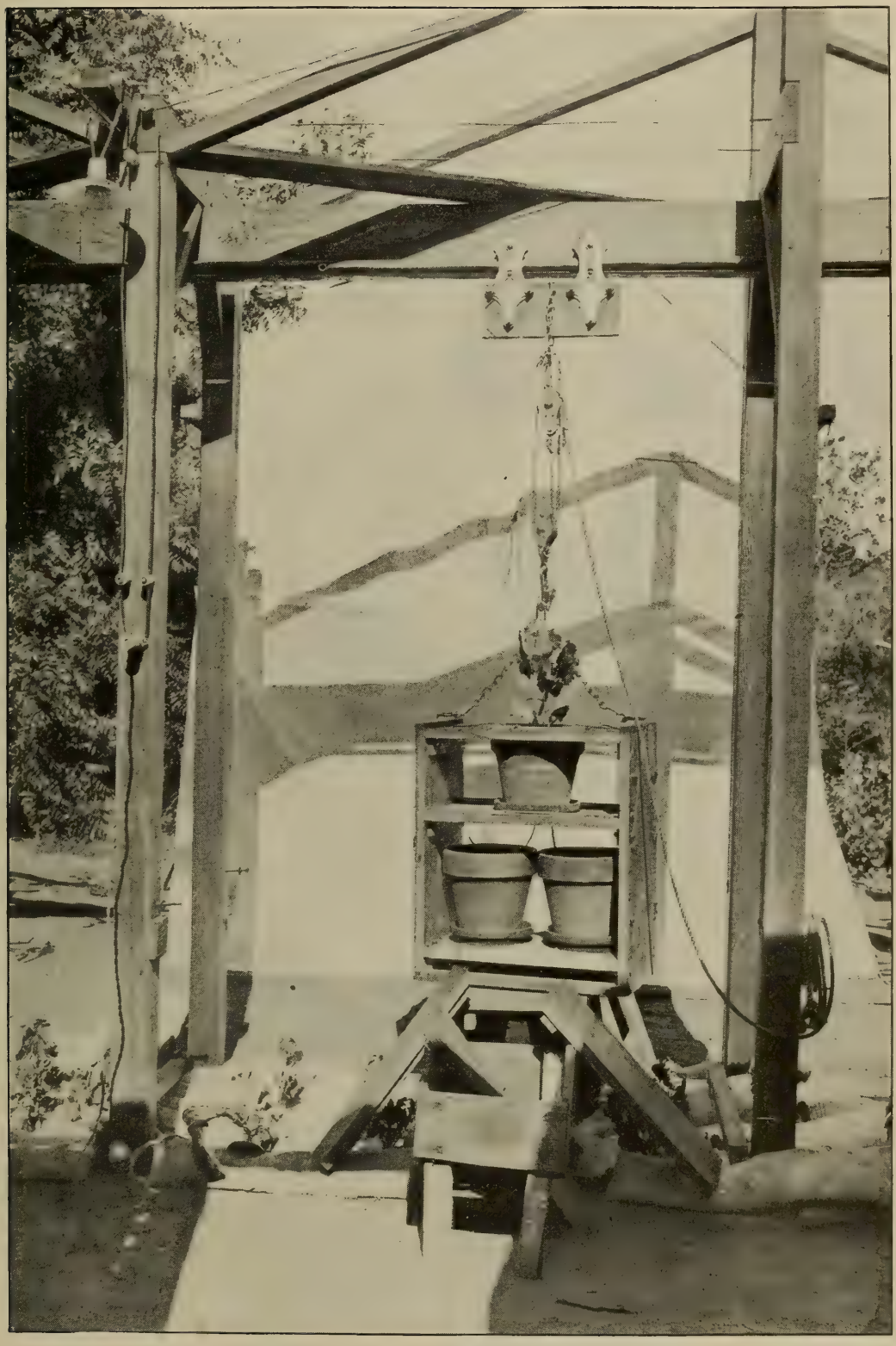


FIG. 2.—Galvanized tin cans used in connection with studies of the underground diffusion of Phylloxera.



THE GRAPE PHYLLOXERA IN CALIFORNIA.

Rearing box drawn up from pit; sides of box removed.

and those in the saucers above were also plugged with cotton. This procedure tended to prevent the phylloxeræ from leaving the exposed portion of the root between the saucer of the upper pot and the surface of the lower. This exposed portion of living root averaged about 4 inches in length.

Scaffolding was built above the trench and a rope and pulleys provided in order that the cages might be raised and set in place on the stand for examination of roots. Electric connections were also provided so as to enable the cages to be examined after dark.

The cages above described were designed by R. L. Nougaret.

DEVELOPMENT OF THE RADICICOLE LARVA.

The young radicicole larva (Pl. IX, *g*, *h*, p. 64), upon hatching from the egg, seeks a place on the root where it may implant its beak and settle down to feed. During the summer some of the newly hatched larvæ desert the vine and go in search of other vines, traveling either through cracks in the soil or over its surface. Newly hatched larvæ are very active at all times and, being flat, can go through very small passages. Considering only those that remain on the vine on which they were born, it is found that the length of time elapsing between the hatching and settling on the root surface varies according to conditions of food at hand. On a decaying root the insect may not find a location for several hours, but if the root is sound the larvæ mostly settle down immediately close by the egg-shells.

A certain percentage of larvæ always wanders about on the roots before finally settling. Many of these make their way outward and downward to the smaller rootlets, while others (mostly of the hibernant generation) in the fall make their way up to the bases of the larger roots and even to the main trunk. Larvæ hatching on a decayed root usually leave it, but occasionally they remain and die of starvation. Observations on pieces of severed roots kept under cellar conditions indicated very little movement of the young larvæ, provided their food was in good condition and they were not too much crowded. In the summer, however, large numbers deserted the roots in a manner similar to that observed in the vineyards, and these were apparently imbued with a wandering instinct.

On vinifera vines young larvæ prefer to settle on succulent parts of roots or rootlets. When they settle on growing rootlets, they generally cause the formation of nodosities, and on the roots of one or more year's growth the formation of tuberosities. They frequently settle on lesions already formed by older phylloxeræ, and sometimes they settle and mature on the root without causing any perceptible lesion. When no lesion is formed, the insects develop

slowly, and as a rule the larger and more fleshy the lesion the more rapid is the growth of the insect thereon. On resistant vines the newly hatched larva rarely fastens on any place except the apex of the rootlet or on a nodosity already formed. On American nonresistant vines the larvæ settle in the main as they do on viniferæ, but on some varieties a decided preference is given to the growing rootlets over the larger roots.

During the years 1911 and 1912 experiments were conducted to determine the growth and development of radicicoles under cellar conditions. Table X summarizes these observations.

TABLE X.—*Summarized records of incubation and development of the radicicole of the grape phylloxera under cellar conditions, during 1911 and 1912, Walnut Creek, Calif.*

Generation.	Incubation period.				Developmental period.				Generation cycle.				Average temperature during period of development.
	Number of individuals.	Maximum.	Minimum.	Average.	Number of individuals.	Maximum.	Minimum.	Average.	Number of individuals.	Maximum.	Minimum.	Average.	
		Days.	*Days.*	*Days.*		*Days.*	*Days.*	*Days.*		*Days.*	*Days.*	*Days.*	*° F.*
1	49	17	10	13.6	181	48	13	29.6	49	56	26	40.5	63
2	58	13	8	10.2	352	61	16	31.7	58	74	25	42.2	64
3	21	12	8	10.1	30	41	16	26.6	21	52	26	37.2	64½
4	10	18	7	13.3	8	24	17	21.9	8	38	24	34.6	64
4[1]					13	208	125	183.0					
5–9[2]	3	12	11	11.3	18	45	14	27.6	3	41	35	37.3	

[1] Hibernating individuals, maturing in 1912.
[2] In 1912 the records extend from Mar. 20 to July 22.

A summary of the observations made on the growth and development of the radicicole on severed root cuttings in the cellar in 1911 and 1912 may be given in brief. The great variation existing in the growth of individuals under the same temperatures, and even on a given piece of root, is resultant entirely from the condition of the food. An aphid living on a callus formation or tuberous lesion develops more rapidly than one living on the normal surface of the same piece of root. Individuals living on vigorous roots develop more rapidly than those on decayed or dying roots. Occasionally a decaying root will send out very fleshy lesions, and these, while they remain fresh, provide ample nourishment for the aphids and enable them to grow quickly. After a root reaches a certain point in decay or dryness the phylloxeræ can no longer develop on it and must seek better food or perish.

The growing period of the aphids recorded in Table X ranged from 13 to 61 days, hibernating individuals excluded. The grand average, hibernants not considered, was 30.57 days, practically one month. That the maximum period may be prolonged is evidenced from an observation made in the summer of 1912, in which a series

of individuals lived from 90 to 105 days on a particularly innutritious piece of root without maturing.

During 1913 two series of further experiments were undertaken. One series was reared in the cellar and the other in an electric incubator, the latter under somewhat higher temperatures. Generations were followed from May to October. Table XI summarizes these observations.

TABLE XI.—*Development of radicicoles of the grape phylloxera, Walnut Creek, Calif., 1913.*

Environment.	Generation.	Number of individuals.	Average period of growth.	Average temperature.
				°F.
Cellar	1	44	37.25	65.1
Do	2	10	32.40	69.8
Incubator	1	15	35.60	65.6
Do	2	24	28.80	71.1
Do	3	3	29.70	70.3

From this table it is noticeable that temperature exerted considerable influence on the growing period of the aphids, and that warmth accelerated their development. In a series of generations reared in 1915 on very nutritious food, recorded under the heading "Maximum and minimum generations yearly" (p. 71), this temperature influence is very apparent. The greater constant warmth in the incubator induced the aphids to remain active later in the fall, after those in the cellar had hibernated. In comparing the 1913 series with those of 1911, it was found that the aphids of the former developed more slowly than did those of the latter, and this notwithstanding the fact that both the series of 1913 enjoyed higher temperatures than did the cellar series of 1911. The roots supplied in 1913 were of much poorer quality than were those supplied in 1911.

Development on living roots, 1913–1915.—During 1913, 1914, and 1915 the habits and development of the radicicoles were observed on living roots of vines growing in cages (Pls. V; VI, fig. 1; VII) kept in a trench where the temperature approximated that obtaining beneath the surface of the soil. As far as the temperature was concerned, the monthly averages ranged less than did those obtaining about 2 feet below the soil surface, but the daily fluctuations were considerably in excess of those in the soil. In the cages the roots were subjected to an average daily fluctuation of about 3° F. in summer and about 2° F. in winter. Two feet beneath the surface, the temperature never fluctuated more than 1° in any given day. As far as could be observed, this temperature fluctuation had little effect on the growth of phylloxeræ, except that it seemed to cause the nodosities to decay more rapidly than they would normally. Occasionally it was noted that some nodosities would dry up quickly after the cage had

been examined and its interior subjected for a few minutes to a temperature several degrees in excess of that obtaining in the trench immediately preceding the examination.

Plate VII illustrates the details of the cages used for observing the phylloxeræ on living roots. By means of the pulley and stand the cages were hauled up and set for examination. It is obvious that only young vines could be used for this work, as 9-inch pots were the largest used. The vines were planted in early spring, certain of the longer roots, drawn through holes cut in the saucer supporting the bottomless upper pot, being planted in the lower pots. Thus about 4 inches of root between upper and lower pots were available for inoculation and observation. At the upper and lower ends of this visible portion the root passed through glass cylinders, and the intervening spaces between the root and cylinder were filled with sand and cotton (sand only was used in the lower cylinders) to prevent the escape of phylloxeræ to the invisible portions of the roots, both above and below. For the viniferæ and nonresistant American vines this, however, failed to answer the purpose in many cases. Out of 22 upper pots, which were examined several months after the exposed roots were inoculated and had suffered more or less severe infestation, 18 developed infestation on their roots, showing that phylloxeræ had found their way up to the roots in the upper pots. Out of 36 lower pots liable to infestation on their roots by reason of the fact that the exposed portions of the roots above were infested, the roots in 9 showed no infestation or indications of any previous infestation, whereas in 13 others infestation occurred which had resulted from larvæ successfully penetrating the lower glass cylinders; in the remaining 14 pots, infestation or signs of previous infestation occurred resulting from wanderers reaching the rootlets by penetrating cracks in the soil. In the case of the resistants, the cylinders of sand and cotton packed between roots and glass were effectual in preventing spread to the invisible portions of the roots. On these vines the infestation was always very slight, and the phylloxeræ exhibited very little desire to travel. On a Champini (rupestris × candicans), on which the phylloxeræ infested only the side rootlets, and which bore only a slight infestation, wandering larvæ entered the soil and infested the rootlets of one of the lower pots, but there was no penetration through the glass cylinders.

As temperature is a factor of importance in the development of the phylloxera, the following comparisons (Table XII) of temperatures are noteworthy, taken (1) inside the cages containing living vines, (2) 2 feet below the soil surface, at a point in the laboratory vineyard a few feet distant from the trench containing the cages aforesaid, and (3) in the laboratory cellar:

TABLE XII.—*Comparative monthly average temperatures; inside cages in trench, 2 feet below soil surface in laboratory vineyard, and in laboratory cellar, Walnut Creek, Calif.*

Month.	Two feet below surface.	In cages in trench.	In laboratory cellar.
1913.	°F.	°F.	°F.
May	.....	[1] 59	.....
June	.....	68	.....
July	76	71	.....
August	77	71	.....
September	77	69	68
October	70.5	65	63
November	64	56	59
December	53	49	56
1914.			
January	54	52	55
February	51	52	55
March	58	56	58
April	62	58	59
May	65.5	63	62
June	70	68	65
July	72.5	72	67
August	74	72	69
September	70.5	66	67
October	66	64	63
November	58.5	56	58
December	50.5	.....	54
1915.			
January	49	.....	54
February	52	.....	55.5
March	57	56.5	57
April	62	57	58
May	63.5	59	60
June	71.5	68	65
July	75.5	73	68
August	75	73.5	69
September	71.5	69	66
October	66	64.5	62

[1] Approximate.

Examination of Table XII indicates that the cellar temperatures showed the least annual variation and that the average temperatures in the soil for every month, except February, 1914, exceeded the corresponding temperatures in the cages. It is probable, leaving other factors out of consideration, that the accumulated excess of heat in the soil over that in the cages throughout one season would produce an extra generation of phylloxeræ, besides prolonging the active development later into the autumn. The summer of 1913 was much warmer than that of the year following. This is borne out by the soil temperature comparisons, but does not appear from the cage temperatures.

To obtain life-history data, the following vines were used: Burger, Muscat, Thompson's Seedless, Mission, Champini, and Grenache. On the Champini the phylloxeræ refused to settle, except on fleshy side-rootlets, but on the others they settled at any point. On the Grenache roots, however, several of the inoculations proved unsuccessful, the young larvæ not settling. On the others, inoculations nearly always proved successful. Inoculations were made by transferring eggs from one root to another with a camel's-hair brush. Since the roots in all cases were vertical, or very nearly so, it happened

occasionally that some of the eggs used in the inoculations dropped off. This was unavoidable, and when egg-laying females were under observation it frequently happened that the eggs dropped down. When more than one female was producing eggs simultaneously on a single root, there even arose doubt as to which certain of the fallen eggs should be credited. For the biological records the first season, 9 vines were used, averaging 3 separate roots each, but since 3 of these roots died, after they were planted, only 24 roots were actually used. Of these 3 were used for rearing gallicole progeny and 5 others were used for nymph production and fertilizer experiments on heavily infested vines, leaving 16 for individual records. In 1914 and 1915, only 4 vines were used each year to continue the individual series.

Many interesting habits were observed, but the behavior of the phylloxeræ in the main did not differ from that observed under cellar conditions upon severed roots. Newly hatched larvæ mostly settled close to the eggshells they had vacated, but if there were any fresh lesions near by, the young larvæ often found their way to them and settled. Occasional movements of older individuals were observed, not only at the time of molting but at any time in the instars. These movements were generally in the direction of more succulent food. Occasionally egg-laying individuals shifted their positions without apparent injury, although this was sometimes followed by a temporary halt in the production of eggs. The production of nymphs occurred from June to October, as in the vineyard. The tendency of the nymphs to crawl up the root just before transforming was noticeable. Most of them could go no farther upward than the cylinder plugged with cotton, and so perforce had to transform into migrants at this point. A small percentage transformed at points farther down the root and did not appear to have made any upward migration. On the heavily infested roots, wanderers appeared from July to October. These roamed around the inside of the compartment, and succeeded in finding their way down through cracks in the soil of the lower pots, and infested the rootlets, especially those growing against the inside of the pots. After irrigation, cracks appeared in the soil around the inside of the pot, furnishing the wandering larvæ access to the rootlets. In no case was this infestation of any great extent, although large numbers of wandering larvæ were observed in several of the cages, and only a very small percentage, presumably, found their way to a new food supply. This fact has an important bearing upon the distribution of the insect as will be noted elsewhere. Although it appeared difficult for the insects to penetrate an inch of sand in the lower glass cylinder, the occurrence of large infestations immediately below the cylinder, coupled with evidences of only slight infestations on the

rootlets around the inside of the pots, showed that such a penetration had occurred. It was obvious in these instances, few though they were, that the heavy infestations could not have resulted from inoculations on rootlets from wanderers, because only a few nodosities occurred on the rootlets, showing a slight wanderer infestation, and not enough time had elapsed in the interim for the infestation present at the date of examination to be produced by so small a company of wandering larvæ. The phylloxeræ had no difficulty in finding their way through the upper cylinder to the root system of the upper pots through layers of cotton and sand each about half an inch thick. On the roots of the upper pot of cage V, Burger, there were, on November 26, 1913, upward of 1,600 hibernants disposed in large clusters on the main root. Since June of that year, the visible portions of four roots below had been well infested. Every one of those 1,600 hibernants was the progeny of phylloxeræ hatched on the visible part of the roots and which had penetrated the upper cylinders. It is obvious that a great many individuals penetrated the cylinders, as the scarcity of lesions showed that the greater part of the infestation was comparatively recent. Apparently a natural law against overcrowding comes into play, and migration was encouraged by the fact that the tuberosities on three of the four roots had become rotted and threatened to decay all the visible portions of those roots. As, on this vine, no infestation other than a few nodosities occurred below the cylinders in the lower pots, it would appear that the heavy migration had been entirely in an upward direction. As far as could be determined, there appeared no reason why the insects could not penetrate the lower cylinders just as easily as the upper ones, so the conclusion is that in most cases they did not make the attempt.

In the instances wherein phylloxeræ had undoubtedly penetrated the lower cylinders they were found to be close to the cylinder as if the packing of sand and cotton had been so loose that no effort was needed for the insect to force its way through. The sand in the upper cylinders, by reason of the weight of earth pressing upon it, always remained well packed and presented a barrier to the progress of the phylloxeræ. That they were able to surmount this barrier is shown by the large numbers present, and indicates that the upward migration was a well-defined movement. The possibility presented itself that infestations on the roots of the upper pots could have originated from wandering larvæ that had penetrated the soil of the upper pots in the same manner as they had obviously done in the lower pots of the cages. The absence of cracks except around the periphery of the soil in the pots and of nodositous infestations on the rootlets below taken in conjunction with the size of the infestations precludes this as the sole source of the inoculations of the upper pots.

Some of the lower pots of the cages were filled with quartz of mixed grades. This was done chiefly for the purpose of experimenting with liquid fertilizers as to the bearing of fertilizing substances upon the behavior of infested vines as an adjunct to similar vineyard experiments. Twelve out of 36 lower pots contained quartz. It was found that the wandering larvæ were able to descend to rootlets growing in the quartz as easily as to those growing in earth. On the other hand, the phylloxeræ were not able to exist on the larger roots in the quartz in appreciable numbers, as it appeared that they could not pass through the quartz when it was packed around the root. This is similar to the condition existing on very sandy soils, wherein the phylloxeræ are unable to travel when the sand becomes packed around the roots.

Table XIII indicates the incubation and development of the radicicoles on the roots of living vines.

TABLE XIII.—*Incubation and development of radicicole of the grape phylloxera on living vines, Walnut Creek, Calif., 1913–1915.*

FIRST GENERATION, 1913.

Individual No.	Date egg deposited.	Date egg hatched.	Incubation period.	Date insect matured.	Growing period.	Total period of development.	Variety of vine and number of cage.	Average temperature.
			Days.		*Days.*	*Days.*		° *F.*
1	Apr. 29	May 14	15	June 8	25	40	Mission VII	60
2	May 28	June 6	9	June 25	19	28	do	67
3	do	do	9	do	19	28	do	67
4	do	do	9	June 26	20	29	do	67
5	do	do	9	June 28	22	31	do	67
6	do	do	9	June 29	23	32	do	67
7	do	do	9	June 30	24	33	do	67
8	do	do	9	do	24	33	do	67
9	do	do	9	do	24	33	do	67
10	June 14	June 22	8	July 5	13	21	Burger VI	69
11	do	do	8	July 8	16	24	do	69
12	do	June 23	9	July 7	14	23	do	69
13	do	June 22	8	July 9	17	25	do	69
14	do	June 24	10	July 14	20	30	do	69
15	June 15	do	9	do	20	29	do	69
16	do	do	9	July 15	21	30	do	69
17	do	June 26	11	July 18	22	33	do	69
18	June 16	do	10	July 21	25	35	do	69
19	June 8	June 17	9	July 9	22	31	Burger V	68
20	do	do	9	do	22	31	do	68
21	do	June 19	11	July 13	24	35	do	69
22	do	do	11	do	24	35	do	69
23	do	June 20	12	July 15	25	37	do	69
24	do	June 17	9	July 7	20	29	do	68
25	do	do	9	July 8	21	30	do	68
26	do	June 18	10	July 2	14	24	do	68
27	do	do	10	do	14	24	do	68
28	do	do	10	do	14	24	do	68
29	do	do	10	July 4	16	26	do	68
30	do	do	10	July 6	18	28	do	68
31	do	do	10	do	18	28	do	68
32	do	do	10	do	18	28	do	68
33	do	do	10	July 7	19	29	do	68
34	do	do	10	do	19	29	do	68
35	May 25	June 4	10	June 19	15	25	do	67
36	do	do	10	June 21	17	27	do	67
37	do	June 5	11	June 23	18	29	do	67
38	do	do	11	June 24	19	30	do	67
39	do	June 6	12	June 25	19	31	do	67
40	do	do	12	do	19	31	do	67
41	do	do	12	June 27	21	33	do	67
42	do	do	12	do	21	33	do	67
43	do	do	12	June 29	23	35	do	68
44	do	June 8	14	July 2	24	38	do	68
45	do	do	14	July 3	25	39	do	68

TABLE XIII.—*Incubation and development of radicicole of the grape phylloxera on living vines, Walnut Creek, Calif., 1913–1915*—Continued.

SECOND GENERATION, 1913.

Individual No.	Date egg deposited.	Date egg hatched.	Incubation period.	Date insect matured.	Growing period.	Total period of development.	Variety of vine and number of cage.	Average temperature.
			Days.		*Days.*	*Days.*		° *F.*
1	June 10	June 20	10	July 8	18	28	Mission VII	68
2	June 11	June 19	8	...do	19	27	.....do	68
3	June 12	...do	7	...do	19	26	.....do	68
4	...do	June 20	8	July 11	21	29	.....do	69
5	June 30	July 6	6	July 20	14	20	.....do	70
6	...do	July 8	8	July 22	14	22	.....do	70
7	...do	...do	8	July 23	15	23	.....do	70
8	...do	...do	8	...do	15	23	.....do	70
9	...do	...do	8	July 31	23	31	.....do	71
10	...do	July 9	9	July 24	15	24	.....do	70
11	...do	...do	9	July 25	16	25	.....do	70
12	...do	...do	9	July 31	22	31	.....do	71
13	July 1	...do	8	Aug. 4	26	34	.....do	71
14	...do	...do	8	Aug. 7	29	37	.....do	71
[1]15	...do	...do	8	Aug. 11	33	41	.....do	71
16	June 30	...do	9	Aug. 8	30	39	.....do	71
17	June 26	July 3	7	July 21	18	25	Burger VI	70
18	...do	July 4	8	July 25	21	29	.....do	70
19	...do	...do	8	July 26	22	30	.....do	70
20	...do	...do	8	...do	22	29	.....do	70
21	...do	...do	8	July 28	24	32	.....do	70
22	...do	July 5	9	July 29	24	33	.....do	70
23	...do	...do	9	July 31	26	35	.....do	70
[1]24	June 27	July 4	7	July 28	24	31	.....do	70
25	...do	July 5	8	July 31	26	34	.....do	70
26	June 30	...do	6	Aug. 8	23	29	Burger V	71
[1]27	...do	July 6	6	Aug. 10	35	41	.....do	71
[1]28	...do	July 7	7	Aug. 12	36	43	.....do	71
[1]29	...do	...do	7	...do	36	43	.....do	71
[1]30	July 1	July 8	7	...do	35	42	.....do	71
[1]31	...do	...do	7	Aug. 13	36	43	.....do	71
[1]32	July 2	...do	6	Aug. 14	37	43	.....do	71
[1]33	...do	July 10	8	Aug. 18	39	47	.....do	71

THIRD GENERATION, 1913.

1	July 23	July 31	8	Aug. 25	25	33	Thompson's Seedless I	71
2	July 28	Aug. 5	8	Aug. 28	23	31	Muscat IV	71
3	July 29	Aug. 7	9	Aug. 30	23	32	.....do	71
4	...do	...do	9	Sept. 1	25	34	.....do	71
5	...do	Aug. 8	10	Sept. 3	26	36	.....do	71

FOURTH GENERATION, 1913–14.

1	Aug. 26	Sept. 3	8	[2]	.....	.....	Thompson's Seedless I	[3]71
2	Sept. 1	Sept. 8	7	Sept. 18	10	17	Champini IX	70
3	...do	Sept. 9	8	Sept. 22	13	21	.....do	69
4	...do	Sept. 10	9	Sept. 30	20	29	.....do	69
5	.....	Sept. 23	.....	Apr. 6	195	.....	Muscat IV	.....
6	.....	...do	.....	Apr. 9	198	.....	.....do	.....
7	.....	Sept. 24	.....	Oct. 24	30	.....	.....do	66
8	.....	...do	.....	Apr. 6	194	.....	.....do	.....
9	.....	...do	.....	Apr. 7	195	.....	.....do	.....
10	.....	...do	.....	May 20	238	.....	.....do	.....
11	.....	...do	.....	Apr. 15	203	.....	.....do	.....
12	.....	Sept. 25	.....	Apr. 24	211	.....	.....do	.....
13	.....	...do	.....	Apr. 28	215	.....	.....do	.....

FIFTH GENERATION, 1914.

1	Apr. 25	May 9	14	May 28	19	33	Muscat IV	62
2	Apr. 26	...do	13	...do	19	32	.....do	62
3	...do	...do	13	June 2	24	37	.....do	63
4	Apr. 27	...do	12	June 1	23	35	.....do	63
5	...do	...do	12	June 2	24	36	.....do	63
6	Apr. 28	...do	11	...do	24	35	.....do	63
7	...do	...do	11	June 3	25	36	.....do	63

[1] Indicates winged migrants. [2] Hibernant. [3] Indicates average temperature of incubation period alone.

TABLE XIII.—*Incubation and development of radicicole of the grape phylloxera on living vines, Walnut Creek, Calif., 1913–1915*—Continued.

SIXTH GENERATION, 1914.

Individual No.	Date egg deposited.	Date egg hatched.	Incubation period.	Date insect matured.	Growing period.	Total period of development.	Variety of vine and number of cage.	Average temperature.
			Days.		*Days.*	*Days.*		° *F.*
1	May 29	June 7	9	June 24	17	26	Muscat IXA	67
2	June 2	June 8	6	July 1	23	29	Grenache IIA	68
3	June 9	June 19	10	July 10	21	31	Muscat IXA	69
4	...do	June 20	11	July 26	36	47	.....do	69
SEVENTH GENERATION, 1914.								
1	June 24	July 3	9	July 23	20	29	Muscat IXA	70
2	...do	July 4	10	July 29	25	35	.....do	71
3	June 25	July 3	8	July 23	20	28	.....do	70
4	...do	July 4	9	July 30	26	35	.....do	71
5	June 26	...do	8	July 28	24	32	.....do	71
6	...do	...do	8	July 30	26	34	.....do	71
7	July 1	July 9	8	July 29	20	28	Grenache IIA	72
8	July 2	July 11	9	...do	18	27	.....do	72
9	...do	...do	9	Aug. 1	21	30	.....do	72
10	July 3	...do	8	Aug. 3	23	31	.....do	72
11	...do	...do	8	...do	23	31	.....do	72
EIGHTH GENERATION, 1914–15.								
1	Aug. 17	Aug. 24	7	Sept. 16	23	30	Muscat XXX	70
2	...do	...do	7	...do	23	30	.....do	70
3	...do	Aug. 25	8	Sept. 26	32	40	.....do	69
4	...do	...do	8	Mar. 26	213	221	.....do	[3] 72
5	...do	...do	8	Mar. 30	217	225	.....do	[3] 72
6	...do	...do	8	Apr. 3	221	229	.....do	[3] 72
7	...do	...do	8	Apr. 4	222	230	.....do	[3] 72
8	...do	...do	8	[4]	.....	.....	.....do	[3] 72
9	...do	Aug. 26	9	[4]	.....	.....	.....do	[3] 72
NINTH GENERATION, 1914–15.								
1	Sept. 16	Sept. 27	11	[4]	.....	.....	Muscat XIX	[3] 72
2	...do	...do	11	Apr. 11	196	207	.....do	[3] 72
NINTH GENERATION, 1915.								
1	Mar. 31	Apr. 19	19	May 22	33	52	Carignan XXIX	57
2	...do	...do	19	May 23	34	53	.....do	57
3	...do	...do	19	May 24	35	54	.....do	57
4	...do	...do	19	May 25	36	55	.....do	57
TENTH GENERATION, 1915.								
1	May 23	June 3	11	June 24	21	32	Carignan XXIX	66
2	May 27	June 6	10	July 1	25	35	Zinfandel XXIIIA	67
ELEVENTH GENERATION, 1915.								
1	July 9	July 15	6	Aug. 10	26	32	Zinfandel XXIIIA	73
2	.....	.....	.....	July 29	.....	.....	Carignan XXIX	.....
3	.....	.....	.....	...do	.....	.....	.....do	.....
TWELFTH GENERATION, 1915.								
1	Aug. 2	Aug. 9	7	Sept. 8	30	37	Zinfandel XXXVI	72
2	...do	Aug. 10	8	Sept. 9	30	38	.....do	72
3	...do	Aug. 9	7	Sept. 10	32	39	.....do	72
4	Aug. 4	Aug. 11	7	...do	30	37	.....do	72
5	Aug. 16	Aug. 24	8	.....	.....	.....	Zinfandel XXIIIA	.....
6	...do	Aug. 25	9	.....	.....	.....	.....do	.....
7	Aug. 17	...do	8	.....	.....	.....	.....do	.....
8	Aug. 18	Aug. 27	9	.....	.....	.....	.....do	.....
9	Aug. 19	...do	8	.....	.....	.....	.....do	.....

[3] Indicates average temperature of incubation period alone.

[4] Died, 1915.

For the first generation, eggs deposited by adult hibernants were secured from a Zinfandel vineyard, and thereafter only eggs deposited in the cages and of known generations were used in the inoculations.

The average growing periods of the summer generations of wingless aphids varied from 34.5 to 18.25 days, but in all except two generations this period ranged between 18.25 and 24.20 days. Individuals varied between 36 and 10 days. The winged forms developed more slowly than the wingless, nine individuals averaging 34½ days. The hibernants developed in an average of 6¾ months.

Eggs were placed for the most part on roots never before infested, and tuberosities usually followed rapidly after the hatching of the larvæ. Nodosities were formed upon side rootlets. The main roots were all between one-sixth and one-third of an inch in diameter.

It was found that about 40 per cent of the larvæ remained on the exposed portions of the roots, the rest finding their way to the other portions. In spring a large percentage and in summer and autumn a smaller percentage of larvæ settled close beside the eggshells from which they had issued. In spring the larvæ did not display a tendency to roam, but in summer and autumn they wandered considerably, especially if the root had begun to decay or was drying too rapidly. Similar conditions occur in vineyards, and it is in summer and autumn that the typical wandering larvæ are found.

Excluding the winged migrants and the hibernated individuals, the summary of the growing period of all the phylloxeræ developing on living roots during the years 1913, 1914, and 1915 is recorded in Table XIV.

TABLE XIV.—*Summary of Table XIII.*

Number of individuals		114
Average period of growth	days	22.15
Maximum period of growth	do	36
Minimum period of growth	do	10

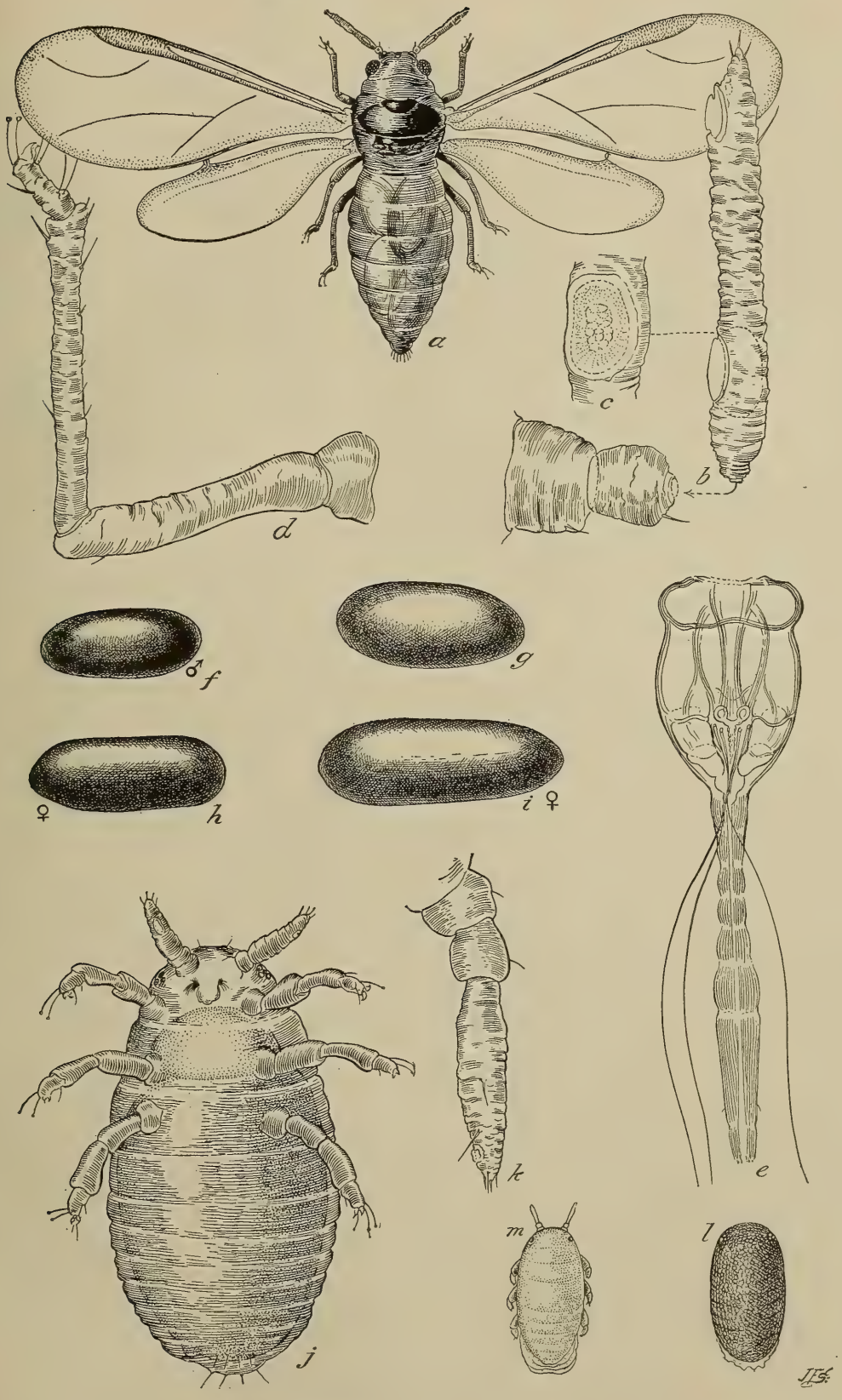
Taking into consideration the individuals removed before they attained their full development, the average growing period is to be estimated at about 25 days. The cellar experiments with severed pieces of roots in 1911 and 1912 combined yielded an average of 30.57 days, and the experiments in the cellar and incubator combined in 1913 averaged 34.16 days. The cellar temperatures of 1911 and 1912 averaged about 1½° F. lower than the combined cage temperatures for the period 1913–1915 for the months from May to October, inclusive. The cellar temperatures for 1913 averaged about 1½° lower than the incubator temperatures for 1913 and about ½° higher than the cage temperatures for that year.

In the cellar and incubator during 1913 the phylloxeræ developed, on the average, more slowly than in the cellar during 1911 and 1912, notwithstanding higher temperatures in 1913. This resulted from the fact that the food supply was much more succulent in 1911 and 1912. Likewise the phylloxeræ developed much more rapidly in the cages in 1913–1915 than in the cellar and incubator combined in 1913, when the temperatures differed slightly (the difference in favor of the cages being about 1° daily). This also was due to the superior food of the living vines. In comparing the phylloxera development in the cellar in 1911–12 with that in the cages in 1913–1915, it would appear that both temperature and food influenced the more rapid development observed in the cages. For 1911 alone the average growing period was 29.37 days. This growth took place on succulent roots, to all appearances as succulent as the living roots upon which were reared the 1913–1915 phylloxeræ, which averaged about a 25-day period, under a temperature averaging 4½° in excess of that obtaining in the cellar in 1911. It would be natural to ascribe the faster growth in the cages to the higher temperatures, but in view of the discrepancies noted above in connection with the 1913 cellar and incubator observations, the writers are inclined to believe that the living roots afforded better nourishment to the phylloxeræ than did the severed roots of 1911 and that the higher temperatures of 1913 had less influence than might appear in bringing about such a difference in the growing periods.

Excepting for a few isolated instances, the phylloxeræ on living roots developed more rapidly on nodosities and tuberosities than on the normal surface of the root. On nodosities development was the most rapid, noticeably more rapid than on tuberosities, and the more fleshy the swelling the more rapid was the aphid's growth.

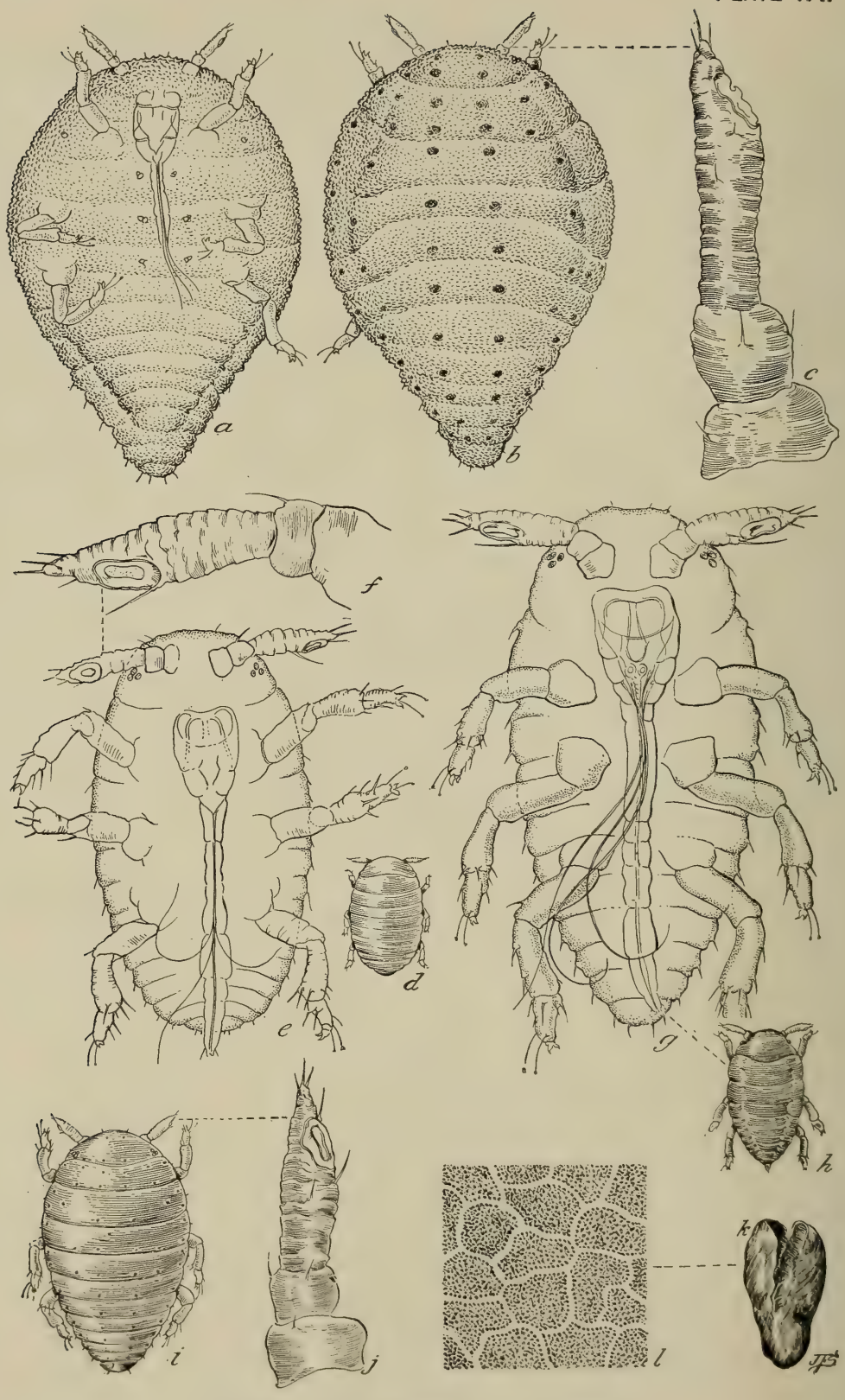
DESCRIPTION OF STAGES.

The egg.—When first laid, the radicicole egg (Pls. VIII, *g;* IX, *k*, *l*) is lemon yellow, about twice as long as wide, oval, both ends rather bluntly rounded, the micropylar end a little more abruptly so. Thirty-six eggs laid by newly matured adults August 30 and September 6, 1911, averaged 0.348 mm. in length and 0.173 mm. in width, with maxima, respectively, of 0.36 and 0.18 mm., and minima, respectively, of 0.34 and 0.17 mm. Of 25 eggs laid by overwintered radicicoles near the end of their laying period, the maximum length was 0.32 mm., the maximum width 0.18 mm., the minimum length 0.20 mm., and the minimum width 0.12 mm., the average length 0.26 mm., and the average width 0.14 mm. Thus it appears that the size of the eggs laid by individuals decreases toward the end of their egg-laying



THE GRAPE PHYLLOXERA IN CALIFORNIA.

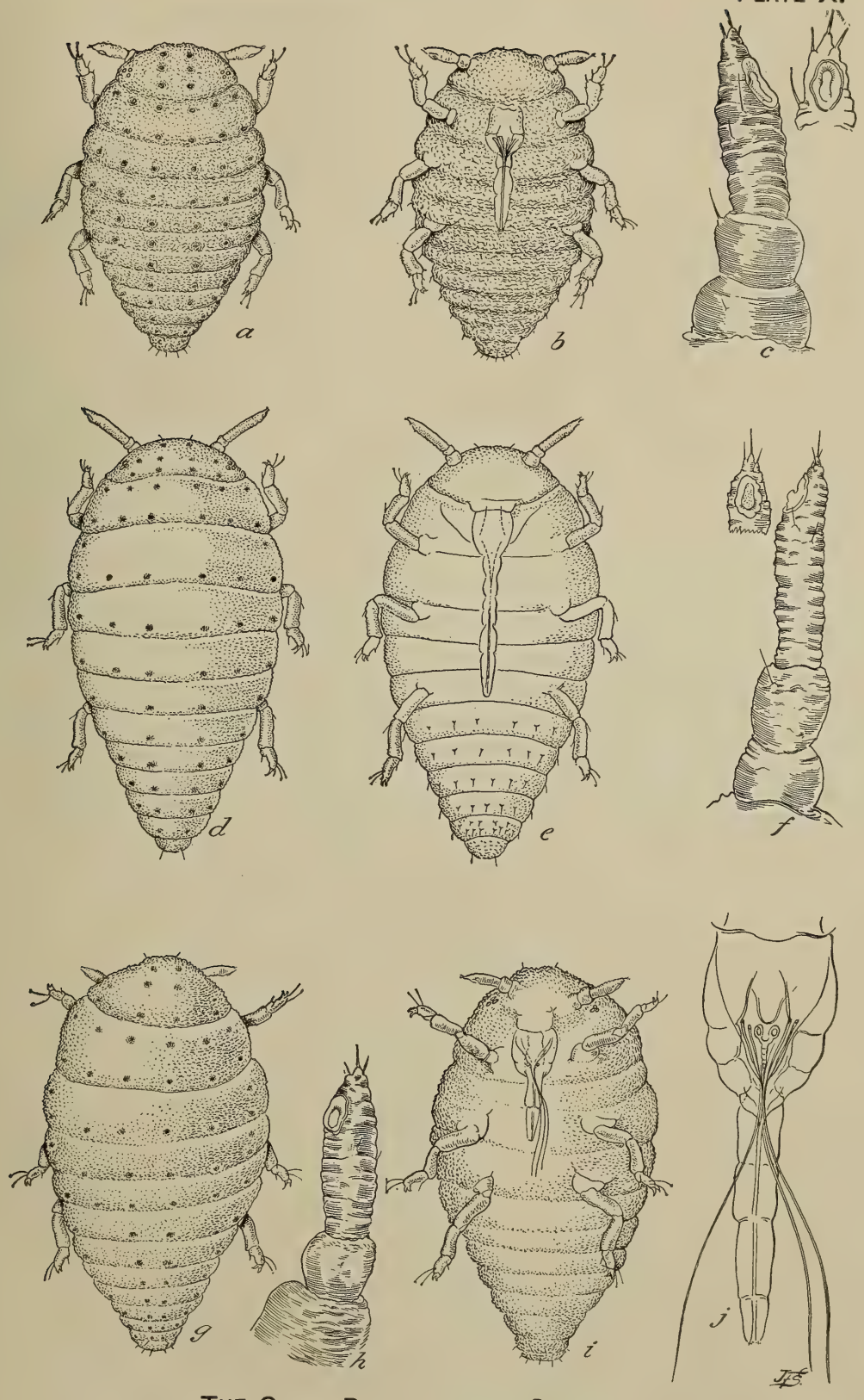
Phylloxera vitifoliae: *a–e,* Winged migrant; *a,* dorsal view; *b,* antenna; *c,* basal sensorium of antennal segment III; *d,* hind leg; *e,* beak; *f,* male egg; *g,* radicicole egg; *h, i,* female eggs; *j, k, l,* sexed female; *j,* enlarged ventral view showing contained winter egg; *k,* antenna; *l,* newly hatched female; *m,* mature male just after casting last skin.



THE GRAPE PHYLLOXERA IN CALIFORNIA.

Phylloxera vitifoliae: *a*, *b*, *c*, Adult radicicole; *a*, ventral view (beak shown telescoped); *b*, dorsal view; *c*, antenna; *d*, *e*, *f*, hibernant larva; *d*, dorsal view; *e*, ventral view; *f*, antenna; *g*, *h*, newly hatched (first-instar) radicicole; *g*, ventral view; *h*, dorsal view; *i*, *j*, second-instar radicicole; *i*, dorsal view; *j*, antenna; *k*, *l*, radicicole egg corium; *k*, whole shell; *l*, section to show structure.

PLATE X.



THE GRAPE PHYLLOXERA IN CALIFORNIA.

Phylloxera vitifoliae: *a*, *b*, *c*, Third-instar radicicole; *a*, dorsal view; *b*, ventral view; *c*, left antenna; *d*, *e*, *f*, prenymph (third instar of winged form); *d*, dorsal view; *e*, ventral view; *f*, left antenna; *g–j*, fourth-instar radicicole; *g*, dorsal view; *h*, left antenna; *i*, ventral view (beak shown telescoped); *j*, beak.

period. Toward the period of hatching the egg becomes darker and the eyespots of the embryo become visible.

The larva.—In hatching, the young larva (Pl. IX, *g*, *h*) splits the eggshell from the micropyle lengthwise to about three-fourths of its length. This splitting is more or less gradual and is caused by the thorax and head of the young phylloxera bursting the shell and then gradually enlarging the crack. The larva poises itself at an angle of 45°, with legs and antennæ appressed to the body, and slowly eases its way out. It seems to rely simply on a slow sidewise body movement to free itself of the shell. When freed, it spreads the appendages and is then able to walk off. The newly hatched larva is of a pale lemon yellow, with dark claret-colored eyes, composed each of three circular facets and placed in the form of the angles of an equilateral triangle. The body segmentation is quite distinct, more so than in later instars. The shape is oval and very flat. The antennæ, as in all forms of the grape phylloxera, are three-jointed. The terminal joint is twice as long as the two basal combined. Near the apex of the third joint occurs a circular sensorium. The beak in early generations reaches to the penultimate or antipenultimate body segment, and in later generations protrudes beyond the caudal segment of the abdomen. The legs and antennæ bear hairs. Table XV gives measurements for five newly hatched individuals.

TABLE XV.—*Measurements of newly hatched radicicoles of the grape phylloxera, Walnut Creek, Calif., Oct. 23, 1914.*

Individual No.	Length of body.	Maximum width of body.	Length of beak.	Length of hind femur.	Length of hind tibia.	Length of antennal joints.			Length of sensorium.
						1	2	3	
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.359	0.176	0.1964	0.0679	0.0571	.....	0.0161	0.0705	.....
2	.327	.179	.2036	.....	.....	0.0169	.0143	.0625	.....
3	.....	.....	.....	.0562	.0429	.0214	.0196	.0680	.....
4	.359	.189	.2152	.0580	.0491	.0232	.0180	.0705	.....
5	.341	.190	.2107	.0566	.0455	.0188	.0188	.0634	0.0231
6	.....	.....	.....	.0554	.0491	.0179	.0152	.0670	.0228

The young phylloxeræ hatching in spring have shorter beaks than those which hatch in the fall, the beaks in spring averaging in length about 0.155 mm.

The first molt does not take place until more than half of the growing period is passed. The molting of the radicicoles is a procedure quite similar in detail to the hatching from the egg. After each molt the individual for about 24 hours is brighter in color than at any other time during the instar. After the first molt the phylloxera changes from oval or suboval to pyriform in shape (Pl. IX, *i*, *j*).

Table XVI gives measurements for four individuals of the second-instar radicicole.

TABLE XVI.—*Measurements of second-instar radicicoles of the grape phylloxera, Walnut Creek, Calif.*

Individual No.	Length of body.	Maximum width of body.	Length of beak.	Length of hind femur.	Length of hind tibia.	Length of antennal joints.			Length of sensorium.
						1	2	3	
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.419	0.234	0.154	0.0625	0.0526	0.0190	0.0204	0.0586	.....
2	.448	.....	.....	.0624	.0518	.0205	.0205	.0589	.....
3	.439	.257	[1].113	.....	.....	.....	.....	.....	.....
4	.499	.270	.168	.....	.....	.....	.....	.....	0.0171

[1] Telescoped.

The roughened tubercular areas on the dorsal surface are more conspicuous after the first molt, and a rapid increase in bulk is apparent during the second instar.

The second, third, and fourth molts occur at practically equidistant periods. Under highest temperatures and optimum food conditions, these instars are passed in about two days apiece. Under a temperature of 58° F. from three to eight days elapse between molts, the average being about five and one-half days.

Table XVII gives the measurements of five individuals of the third instar.

TABLE XVII.—*Measurements of third-instar radicicoles of the grape phylloxera, Walnut Creek, Calif.*

Individual No.[1]	Length of body.	Maximum width of body.	Length of beak.	Length of hind femur.	Length of hind tibia.	Length of antennal joints.			Length of sensorium.
						1	2	3	
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.592	0.303	0.178	0.0699	0.0607	0.0202	0.0321	0.0616	0.0
2	.524	.312	.164	.....	.....	.0252	.0207	.0568	.0144
3	.522	.332	.179	.0739	.0622	.....	.....	.....	.....
4	.649	.355	.155	.0732	.0687	.0241	.0205	.0634	.....
	.....	.....	.....	.0758	.0660	.0197	.0187	.0589	.0177
5	.648	.371	.145	.0741	.0692	.0206	.0194	.0598	.0186
6	.....	.....	.....	.....	.....	.....	.....	.....	.0190

[1] Individuals 1–3, newly molted; 4, two days after molt; 5, three days after molt.

During the third instar (Pl. X, *a*, *b*, *c*) the increase in bulk continues rapidly. The dorsal tubercular areas are larger than in the previous instar, but in color and shape no differences appear.

Table XVIII indicates the measurements of seven individuals of the fourth (penultimate) instar.

TABLE XVIII.—*Measurements of fourth-instar radicicoles of the grape phylloxera, Walnut Creek, Calif.*

Individual No.[1]	Length of body.	Maximum width of body.	Length of beak.	Length of hind femur.	Length of hind tibia.	Length of antennal joints.			Length of sensorium.
						1	2	3	
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.919	0.517	.....	0.0848	0.0687	0.0321	0.0259	0.0669	.....
2	.851	.528	.....	.....	.....	.0321	.0277	.0571	.....
3	.824	.579	.....	.0830	.0749	.0276	.0241	.0768	0.0212
4	.615	.500	0.172	.....	.....	.0306	.0261	.0748	.0167
5	.....	.....	.162	.....	.....	.0297	.0248	.0721	.0162
6	.753	.426	.160	.0802	.0671	.....	.....	.....	.....
7[2]	.700	.....	.....	.....	.....	.....	.....	.....	.....

[1] Individuals 1–3 were measured toward the end of the instar, and individuals 4–7 very shortly after molting.
[2] Maximum height, 0.3 mm.

A very obvious growth takes place during the fourth instar (Pl. X, *g–j*). At the end of this instar the phylloxera casts its last skin and issues therefrom as an adult. The adults, except immediately following the molt, are never as pale as the immature forms. They may be distinguished from fourth-instar individuals by two longitudinal furrows on the thorax and by the relatively larger dorsal tubercular areas. The color varies from a light green to a dark purplish brown in living specimens. This variation is to a great degree dependent on the food supply. On fresh, fleshy nodosities the insects mostly are pale green with the tubercular areas very noticeable. On tuberosities, or on the normal surface of a vigorous root, the color is yellowish green, olive green, or light brown, with the tubercular areas often less evident.

On roots of poor quality the adults are brown or orange and the tubercular areas hardly perceptible to the naked eye. After weeks of egg production old adults become brown or purplish brown. In shape the adults while not engaged in egg laying are hemispherical or short oval, about equally rounded at either extremity, but while an egg is being passed the insect assumes a pyriform shape and the caudal end is much tapered and extended.

Mature radicicole.

Pl. IX, *a, b, c.*

Color varying from pale green and pale yellow to deep purplish brown, dependent on character of food and age of individual; shape hemispherical, short oval, pyriform while passing the ova; body obscurely glabrous, often appearing to be coated on the dorsum with a very fine whitish powder; under side of abdomen paler than upper. Body about twice as long as wide, widest at middle of mesothorax; highest at about cephalic third; body flattening both cephalad and caudad from this point. Head with dusky central area; eyes dark red, each composed of three circular facets, arranged in form of an equilateral triangle; antennæ pale, not quite reaching posterior margin of head, composed of three joints, of which the two basal are subequal in length but

joint 1 wider than joint 2; third joint about twice as long as the two basal combined and bearing a single oval sensorium near apex; all three joints bearing hairs. Beak pale, base and tip shining and dusky, reaching to second or third abdominal tergite; in specimens examined after they had transfixed the beak into the roots, this organ appears to be shorter, due to the telescoping of the sheath from the action of transfixing.

Mesothorax largest segment of body, twice as long as prothorax, which is next largest; mesothorax divided into two sections by transverse fold. Thoracic segments having median portions raised above lateral portions by means of two longitudinal curved folds. Metathorax very similar above to any of first five abdominal segments. Legs in pale specimens slightly darker than abdomen, coxæ dusky.

Sixth abdominal segment produced conically at each of its posterior angles and narrowed basally; caudal segment twice as long as broad, bluntly rounded, with a small central emargination and fringed with a marginal row of pale weak hairs.

The dorsum of the body bears six longitudinal rows of dusky circular tubercular areas, which under magnification appear as thickenings and roughenings of the epidermis, and each of these is surmounted by a single spine.

Table XIX gives measurements of the adult radicicole.

TABLE XIX.—*Measurements of mature radicicole of the grape phylloxera, Walnut Creek, Calif.*

Individual No.	Length of body.	Maximum width of body.	Length of beak.	Length of hind femur.	Length of hind tibia.	Length of antennal joints.			Length of sensorium.
						1	2	3	
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.854	0.502	.....	0.0795	0.0786	0.0223	0.0251	0.0661	0.0224
				.0804	.0759	.0252	.0243	.0660	.0195
2	.878	.549	0.281	.0839	.0748	.0260	.0230	.0673	.0196
3	1.011	.584	.....	.0875	.0768	.0197	.0230	.0705	.0205
4	.997	.558	.....	.....	.....	.....	.....	.....	.....
5	.942	.593	.....	.....	.....	.....	.....	.....	.....
6	.783	.507	.....	.....	.....	.....	.....	.....	.....
7	.778	.503	.....	.....	.....	.....	.....	.....	.....
8	.763	.455	.....	.....	.....	.....	.....	.....	.....
9	.734	.433	.....	.....	.....	.....	.....	.....	.....
10	.714	.448	.....	.....	.....	.....	.....	.....	.....
11	.712	.392	.....	.....	.....	.....	.....	.....	.....
12	.686	.408	.....	.....	.....	.....	.....	.....	.....
13	.631	.416	.....	.....	.....	.....	.....	.....	.....
14	.582	.352	.....	.....	.....	.....	.....	.....	.....

Measurements of beaks from nine adult hibernants were made March 18, 1915. Of these six, fixed in the root tissue, measured 0.276, 0.243, 0.260, 0.252, 0.198, and 0.179 mm., respectively. The other three, not fixed since casting their last skin, measured 0.329, 0.317, and 0.299 mm., respectively. The basal joints of the rostrum are telescoped when the beak is thrust into the root.

It is obvious from an inspection of Table XIX that the adult radicicoles vary greatly in size. This variation occurs whatever kind of food supply the phylloxeræ are getting, although the average size is larger on good succulent food than on that of poorer quality. Individuals 5 to 14 in Table XIX were all taken the same day (Mar. 18)

from equally succulent pieces of severed roots. They show a considerable variation in dimensions, but, being hibernants, their average dimensions are less than those of the summer generations under equally favorable food-supply conditions; for among the hibernant adults there always may be found a considerable number of small-sized individuals which evidently owe their physical inferiority to the vicissitudes of the long hibernation period. Radicicoles raised on fleshy and succulent nodosities attain an average size of about 1 by 0.55 mm., those raised during the summer on other parts of the root system average slightly less, and the hibernant individuals average 0.75 by 0.50 mm.

Radicicole molts.—The radicicole, in common with other forms of the phylloxera, invariably molts four times.

In 1914 and 1915 records of molts were taken, and Tables XX and XXI indicate molting records of 20 individuals reared on severed roots in the laboratory cellar during the summer of 1914.

TABLE XX.—*Molting records of 20 radicicoles of the grape phylloxera, summer of 1914, Walnut Creek, Calif.*

Individual No.	Date egg batched.	Date of first molt.	First instar.	Date of second molt.	Second instar.	Date of third molt.	Third instar.	Date of fourth molt.	Fourth instar.	Total growing period.	Average temperature.
			Days.		*Days.*		*Days.*		*Days.*	*Days.*	°*F.*
1	July 22	Aug. 6	15	Aug. 9	3	Aug. 11	2	Aug. 14	3	23	68
2	...do....	Aug. 7	16	...do....	2	...do....	2	...do....	3	23	68
3	July 23	Aug. 6	14	...do....	3	Aug. 13	4	Aug. 16	3	24	68
4	...do....	...do....	14	.....	.....	.....	.....	.....	.....	.....	.....
5	July 24	Aug. 7	14	Aug. 9	2	Aug. 11	2	Aug. 14	3	21	68
6	July 25	Aug. 4	10	Aug. 6	2	Aug. 8	2	Aug. 9	1	15	68
7	...do....	...do....	10	...do....	2	...do....	2	Aug. 11	3	17	68
8	...do....	Aug. 5	11	Aug. 8	3	Aug. 9	1	...do....	2	17	68
9	...do....	...do....	11	...do....	3	Aug. 11	3	Aug. 13	2	19	68
10	...do....	...do....	11	Aug. 9	4	Aug. 12	3	Aug. 14	2	20	68
11	...do....	Aug. 6	12	Aug. 8	2	Aug. 11	3	Aug. 13	2	19	68
12	...do....	...do....	12	...do....	2	...do....	3	Aug. 14	3	20	68
13	...do....	Aug. 5	11	...do....	3	Aug. 9	1	Aug. 11	2	17	68
14	...do....	Aug. 7	13	Aug. 10	3	.....	.....	.....	.....	.....	.....
15	...do....	Aug. 8	14	...do....	2	Aug. 13	3	Aug. 15	2	21	68
16	...do....	...do....	14	...do....	2	Aug. 12	2	...do....	3	21	68
17	...do....	Aug. 9	15	Aug. 13	4	Aug. 15	2	Aug. 18	3	24	68
18	...do....	Aug. 11	17	Aug. 14	3	Aug. 17	3	...do....	1	24	68
19	...do....	Aug. 13	19	Aug. 20	7	Aug. 24	4	Aug. 28	4	34	68
[1] 20	...do....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

[1] Hibernant died unmolted Oct. 11.

TABLE XXI.—*Summary of Table XX.*

	Average period.	Maximum period.	Minimum period.
	Days.	*Days.*	*Days.*
First instar, 19 individuals	13.3	19	10
Second instar, 18 individuals	2.9	7	2
Third instar, 17 individuals	2.5	4	1
Fourth instar, 17 individuals	2.5	4	1
Developmental period, 17 individuals	21.2	34	15

All the individuals utilized in this experiment were reared on severed pieces of roots in a petri dish under cellar conditions. Individuals 19 and 20 lived on a much poorer root than the others, and thus is explained the relatively slow growth (34 days) of the one and the early hibernation of the other. Individuals 4 and 14 moved away after their first and second molts, respectively. It will be observed from the summary that the average period of the first instar (13.3 days) is considerably longer than is that of the three succeeding instars combined (7.9 days). The comparative periods of the instars are about constant; that is, an individual with a short first instar will have short succeeding instars and one with a long first instar will have long succeeding instars.

The records of Table XX were made in midsummer at a temperature of 68° F. In the soil at such a time of the year the temperature is higher and the development of the phylloxera more rapid, while in spring and late fall the development is correspondingly slower. The developmental period of the hibernated larvæ varies greatly, not so much from temperature as from other causes. There is an average period of two and one-half weeks from the commencement of feeding to the shedding of the first skin, and after that an average period of three weeks between the casting of the first skin and the shedding of the fourth, the second, third, and fourth instars occupying an average space of a week each. As summer progresses the development of the radicicoles becomes accelerated, as may be observed from Table XXII.

TABLE XXII.—*Molting records of radicicoles of the grape phylloxera, March to July, 1915, Walnut Creek, Calif.*

Individual No.	Date egg hatched.	Date of first molt.	First instar.	Date of second molt.	Second instar.	Date of third molt.	Third instar.	Date of fourth molt.	Fourth instar.	Total growing period.	Average temperature.	Generation.
			Days.		*Days.*		*Days.*		*Days.*	*Days.*	°*F.*	
1	Mar. 19	Apr. 3	15	Apr. 10	7	Apr. 16	6	Apr. 22	6	34	58.25	A.
2	...do...	Apr. 7	19	...do...	3	...do...	6	...do...	6	34	58.25	A.
3	...do...	Apr. 8	20	Apr. 13	5	Apr. 18	5	Apr. 23	5	35	58.25	A.
4	...do...	Apr. 10	22	Apr. 17	7	Apr. 21	4	Apr. 25	4	37	58.25	A.
5	May 11	May 27	16	May 30	3	June 1	2	June 5	4	25	61	B.
6	...do...	...do...	16	...do...	3	...do...	2	...do...	4	25	61	B.
7	May 23	June 7	15	June 10	3	June 13	3	June 16	3	24	63	B.
8	June 16	June 27	11	June 30	3	July 1	1	July 4	3	18	65	C.
9	...do...	June 30	14	July 2	2	July 4	2	July 9	5	23	65	C.
10	...do...	July 3	17	July 6	3	July 9	3	July 10	1	24	65	C.

The individuals enumerated in Table XXII were reared under cellar conditions on equally succulent pieces of severed roots. Table XXII, both by itself and taken in conjunction with Tables XX and XXI, indicates the influence of temperature upon the development of the radicicole under equal food conditions. Under a temperature of 58.25° F. the period of growth averaged 35 days, under an aver-

age of 61.75° F. this period was 24.75 days, under 65° F. it was almost 22 days, and under 68° F. it was lowered to 20.3 days (individual on unthrifty root disregarded). Under the lower temperatures all the instars are correspondingly longer than under the highest midsummer temperature, but the first instar is proportionately less lengthened than are those following it, a phenomenon that becomes quite apparent in the case of the hibernants, provided their first instar be considered in a restricted sense to cover only that period between the time when they commence feeding in spring and the date of the first molt. The hibernant feeds for two and one-half weeks before and for three weeks after its first molt, while in midsummer the larva feeds for 13 days before and for 8 days after its first molt before it matures.

MAXIMUM AND MINIMUM GENERATIONS YEARLY.

In 1911 overwintered adult radicicoles matured at the end of April, throughout May and June, and as late as July 7. Eggs of the first generation were deposited from the end of April until October 1. From the earliest eggs there followed seven complete generations from hibernant to hibernant inside of the one year. No observations were taken of the hatching of the late eggs deposited by late first-generation phylloxeræ in September, but in the light of contemporary observations on individuals of later generations there is no doubt that a certain percentage of these late eggs would have hatched into hibernants, thus giving a minimum of one generation per annum. In 1915, taking advantage of a hibernant which matured exceptionally early in the spring, it was possible to secure eight complete generations within the year. Table XXIII records the development of these generations.

TABLE XXIII.—*Maximum series of generations of radicicoles of the grape phylloxera, reared under cellar conditions, Walnut Creek, Calif., 1915.*

Generation No.	Date of egg deposition.	Date of egg hatching.	Date insect matured.	Generation cycle.	Temperature (average).
				Days.	*° F.*
1[1]	—— —, 1914	—— —, 1914	Feb. 26, 1915	.....	.....
2	Feb. 26, 1915	Mar. 19, 1915	Apr. 22, 1915	55	58.25
3	Apr. 27, 1915	May 11, 1915	June 5, 1915	39	61.20
4	June 7, 1915	June 16, 1915	July 4, 1915	27	64.50
5	July 5, 1915	July 14, 1915	July 28, 1915	23	69.50
6	July 28, 1915	Aug. 4, 1915	Aug. 23, 1915	26	68.50
7	Aug. 23, 1915	Aug. 31, 1915	Sept. 23, 1915	31	67.00
8	Sept. 25, 1915	Oct. 7, 1915	Oct. 27, 1915	32	62.50
9[1]	Oct. 27, 1915	Nov. 10, 1915	—— —, 1916	.....	.....

[1] Hibernant.

In this experiment the food supplied to the phylloxeræ was, as far as one could judge, of equal quality and very nourishing. The influence of temperature is noticeable.

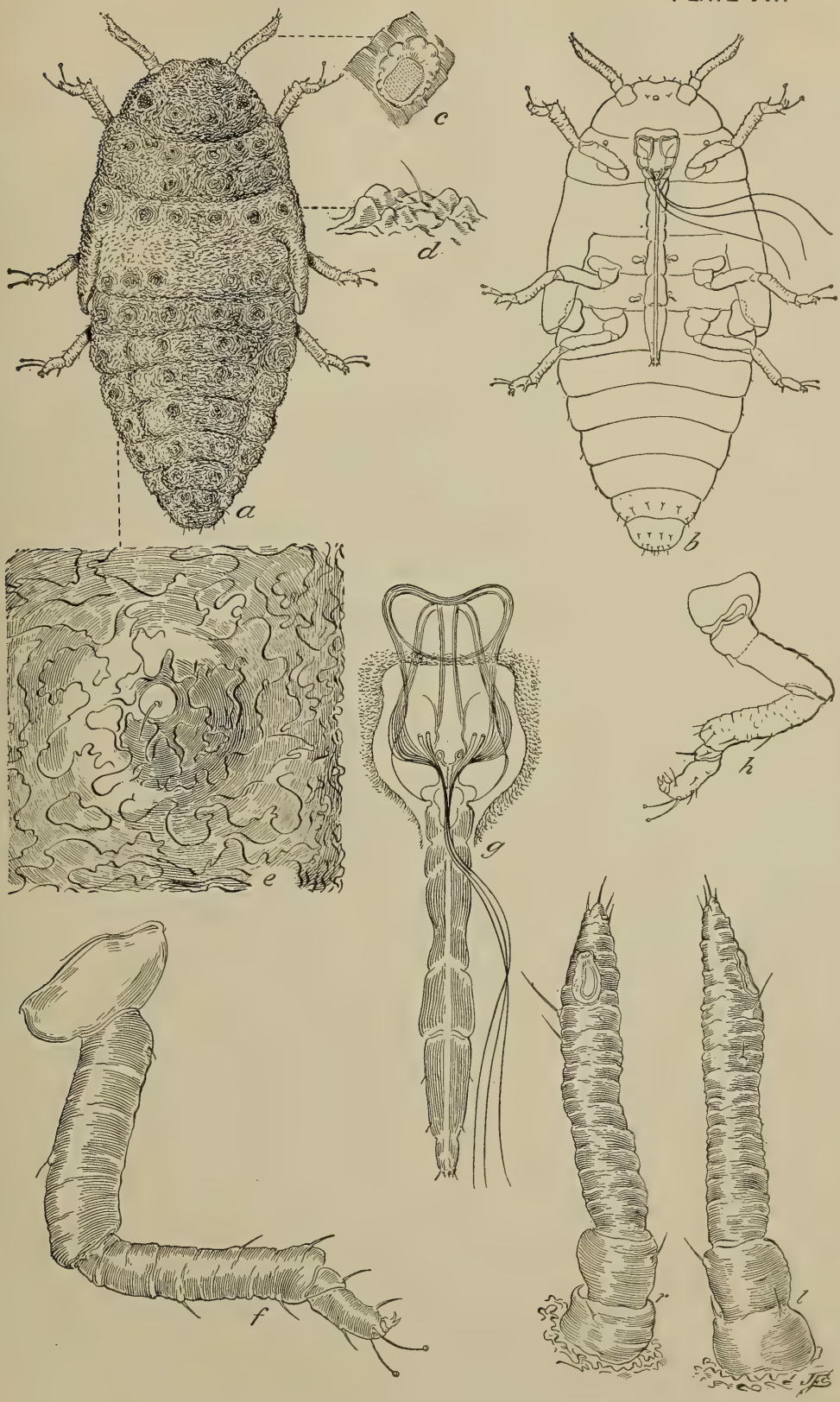
In observations with phylloxeræ developing on living vines there were secured in a period of three years 13 generations, an average of a little over four generations a year, but had the earliest eggs of each generation been successfully utilized, and had it been possible to start the first of the three seasons with the earliest eggs procurable in the vineyards, there is no doubt that six, and possibly seven, generations could have been developed each year.

Considering that the hibernant generation occupies a period of half a year, it is apparent that if seven generations are to be produced in a year, the other six must be passed in an average maximum of one month apiece. In summer phylloxeræ have been reared from egg deposition to maturity in 21 days, but in April, May, and October the cycle rarely falls below 35 days, so that in the six-month period, April 15 to October 15, the average maximum cycle is roughly 30 days. Thus, in the vineyard, even on vines that move early in spring, it is probable that more than seven generations rarely take place in 12 months. The period, October 15 to April 15, best represents the cycle of the wintering generation, although these dates are somewhat arbitrary.

Under vineyard conditions it is always possible to find hibernant phylloxeræ as late as the beginning of June. It is also possible to find insects going into hibernation as early as September 20. Since the mature radicicoles deposit eggs for periods exceeding three months, it can be seen readily that the latest eggs of a radicicole hibernant maturing in June may develop larvæ which proceed to hibernate. A minimum of one generation a year thus may occur. Observations indicate that this minimum of one generation is not common, even on moribund vines with innutritious roots.

WANDERING RADICICOLE LARVÆ OR "WANDERERS."

By the term "wanderers" are designated those forms (almost all newly hatched larvæ) which forsake the root on which they issued from the egg and seek to reach the surface of the soil or to pass through the soil itself, with the object of finding new food. Those that strive to reach the surface exhibit in their efforts a very marked positive phototropism. It would appear that their first movement is simply one of ascending the root and that as soon as they are brought into the focus of a ray of light they immediately make it their goal, and thus finally ascend to the surface. The initial wandering movement comes irrespective of light rays, but as soon as these rays are brought to bear the activity is very pronounced. The conclusion is that the production of individuals destined to wander is due to a combination of influences more than to any single influence—the crowded condition of the phylloxeræ in summer, the decaying of the roots, especially the fleshy surface rootlets, found on



THE GRAPE PHYLLOXERA IN CALIFORNIA.

Phylloxera vitifoliae: *a*, Nymph, dorsal view; *b*, outline ventral view of same; *c*, enlarged sensorium on antennæ; *d*, enlarged tubercle with spine; *e*, microscopic structural view of tubercle; *f*, hind leg; *g*, beak showing structure; *h*, middle leg; *r*, right antenna; *l*, left antenna.

phylloxerated vines, the rising temperature, and the intrinsic vigor of the vine encouraging emigration.

Apparently the young produced from the eggs deposited by overwintered females do not become wanderers, but those of later generations may, and many wandering larvæ produced late in the autumn settle on roots and hibernate.

Wandering larvæ play an important part in the diffusion of phylloxera.

THE NYMPH AND WINGED FORM.

DEVELOPMENT.

The individuals which are destined to become winged are termed in their third instar "prenymphs" and in their fourth instar "nymphs." They are produced from eggs deposited by adult radicicoles, and until after their second molt differ in nowise from the individuals destined to remain wingless; neither is there any difference in the eggs from which the two types hatch. In their third instar the prenymphs (Pl. X, *d*, *e*, *f*) differ from the radicicoles of that instar in that the former have more elongate and narrower bodies and longer antennæ and legs. The prenymphs are generally pale greenish yellow, and their appendages appear quite dusky in comparison. Table XXIV gives measurements of four prenymphs.

TABLE XXIV.—*Measurements of prenymphs of the grape phylloxera, Walnut Creek, Calif.*

Individual No.[1]	Length of body.	Maximum width of body.	Length of beak.	Length of hind femur.	Length of hind tibia.	Length of antennal joints.			Length of sensorium.
						1	2	3	
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.805	0.405	0.357	0.0948	0.0821	0.0330	0.0268	0.0839	0.0196
				.0939	.0839	.0321	.0277	.0889	.0193
2	.660	.325	.193	.0946	.0713	.0306	.0279	.0973	.....
						.0306	.0279	.0919	.....
3	.541	.300	.186	.....	.....	.....	.....	.....	.....
4	.555	.284	.....	.....	.....	.....	.....	.....	.....

[1] Individual 1, just before molting into nymph; individuals 2 to 4, very shortly after molting into prenymphs.

The prenymph molts into the nymph or pupa. The pupa is the longest of all forms of the insect and is easily discernible on the root by the presence of wing pads, even just after it has molted from the prenymphal form, and has a greenish color. Immediately after the skin is shed, these wing pads are yellow, but very quickly they become gray or blackish. During the first few days of the nymphal instar the insect is green or greenish yellow, and the compound eyes are indiscernible, but as it grows it lengthens, becomes constricted in the region of the metathorax, and turns orange, the mesothorax, however, remaining paler than the rest of the body. The compound

eyes show their red pigment and soon become prominent. Legs and antennæ are relatively long, and the femora exceed the tibiæ in length. At all times the rows of tubercular areas on the dorsum are well marked. During the nymphal instar the insect shows a very considerable growth; the newly molted individuals are quite flat, but full-grown nymphs are roughly cylindrical.

DESCRIPTION OF STAGES.

The nymph or pupa, full grown.

Pl. XI; text fig. 9, p. 85.

General color orange or orange yellow; anterior part of mesothorax and mesosternum whitish, or at least always noticeably paler than the rest of body. Antennæ pale yellow, extended but little beyond anterior margin of prothorax. Compound eyes and ocelli dark red; former composed of large number of facets. Head and abdomen bearing 4, thorax 6 longitudinal rows of dark tubercular areas (coarse roughening of epidermis), each surmounted by a spine; wing pads dark gray, grayish black, or rarely jet black; legs pale yellow, often with a dusky cast; abdomen with 7 visible segments, mesothorax apparently bisected by a transverse fold; beak very pale yellow, reaching to posterior coxæ.

Measurements of 6 individuals are given in Table XXV.

TABLE XXV.—*Measurements of nymph of the grape phylloxera, Walnut Creek, Calif.*

Individual No. [1]	Length of body.	Maximum width of body.	Length of beak.	Length of hind femur.	Length of hind tibia.	Length of antennal joints.			Length of sensorium.
						1	2	3	
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	1.102	.....	0.3295	0.1500	0.1366	.....	0.0402	0.1536	0.0223
	.....	.....	.....	.1464	.1384	0.0339	.0350	.1545	.0224
2	.889	.....	.3600	.1419	.1321	.....	.0331	.1455	.0230
	.....	.....	.....	.1438	.1304	.....	.0332	.1455	.0254
3	.957	.507	.3339	.1089	.1071	.0321	.0339	.1179	.0223
	.....	.....	.....	.....	.....	.0304	.0295	.1184	.0232
4	.851	.....	.....	.....	.....	.....	.....	.....	.....
5	.798	.511	.2695	.1389	.1252	.0315	.0309	.1577	.0198
6	.725	.....	.....	.....	.....	.....	.....	.....	.....
7	1.121	.558	.....	.....	.....	.....	.....	.....	.....
8	1.197	.569	.....	.....	.....	.....	.....	.....	.....

[1] Individuals 1, 7, and 8 at end of stage; 4, 5, and 6 at beginning of stage; 2 and 3 about middle of stage

Newly molted nymphs average about 0.78 mm. in length and mature nymphs about 1.1 mm. The nymphs are always more active than the immature wingless forms, wandering larvæ excepted. Their eyes are well developed, as in the winged insect, and they have the ocelli found in that form. The third joint of the antennæ bears a single sensorium corresponding to the apical one of the migrant, and as the last molt approaches the migrant antennæ show through the nymphal skin, and thus the nymphal antennæ appear to bear two sensoria.

The adult instar of the winged form shows what is probably the most highly developed form structurally of the phylloxera. The winged insect is, on the average, slightly shorter than the full-grown nymph. The antennæ are longer than those of the previous instar and bear two sensoria of about equal size. The comparatively large wings are weakly veined but necessitate strong muscles in the interior of the thorax. The legs are quite long and the tibiæ exceed the femora in length. As the migrant sheds the nymphal skin, pushing it back and moving about its appendages, the wing pads appear as little white rolls; the mesothorax is shining green, the head and abdomen bright orange. The wings unroll as the skin is being passed off the abdomen. As soon as it is entirely shed the insect moves off and then pauses while the wings assume their final shape and position, but remain whitish, hyaline, and limp. Soon, however, the wings dry and the thorax hardens and darkens until it is almost black. The head, prothorax, and abdomen remain orange, the head with a grayish luster. The molting process occupies about 50 minutes.

The adult winged form.

Pl. VIII, *a–e.*

General color orange or yellowish brown or gamboge yellow; head a little dusky on the anterior half, especially the cephalic margin (front); ocelli dark red; eyes brighter red than ocelli, compounded of many facets; ocular tubercle small; antennæ with three joints, not quite reaching the anterior margin of the mesothorax, pale yellow, with apical fourth of joint 3 dusky gray; third joint much the longest, considerably over twice as long as first two combined, somewhat constricted beyond the basal sensorium and at extreme base; posterior half of head, prothorax, and abdomen orange, yellowish brown, or gamboge.

Thoracic lobes, scutellar lobes, scutellum, and mesosternum dark gray or blackish; legs pale yellow, tarsi duskier; wing insertions, stigma, and veins gray (at first greenish); stigma equal in length to about one-fourth of wing.

First discoidal arising from subcosta not far from basal angle of stigma, stout, not attaining the wing margin by a space equal to one-fifth its length; second discoidal faint, arising from the first vein or discoidal a little before its center and almost reaching the wing margin at a point a little nearer to the apex of the third discoidal than to that of the first; third discoidal faint, arising from first vein close to its base and continuing with a double shallow curve almost to the wing apex (the basal half of this vein generally obsolete). Lower wings with the costal vein running parallel to the anterior margin for its whole length; cauda bluntly rounded, bearing a fringe of hairs; beak slender, pale yellow, and almost reaching to second coxæ; two longitudinal oval sensoria on the third antennal joint; basal sensorium situated at basal third of joint, apical sensorium close to apex of joint. Wings borne horizontally, apparently the positions interchangeable, the right pair sometimes overlapping the left and vice versa. Abdomen widest at second and third abdominal segments, where it is wider than the thorax, and about as long as head and thorax combined. Body about as high as wide, not at all flat.

Table XXVI gives the measurements from 8 individuals.

TABLE XXVI.—*Measurements of the winged migrant of the grape phylloxera, Walnut Creek, Calif.*

	1	2	3	4	5	6	7	8
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Length	1.101	.....	.....	.....	0.906	.....	.....	0.900
Width (abd. seg. 3)	.428	.....	.....	.....	.317	.....	.....	.390
Width (thorax)	.333	.....	.....	.....	.309	.....	.....	.....
Antennal joints, length:								
1	.....	0.0384	0.0375	0.0321	.0320	0.0393	.....	.....
2	.....	.0402	.0393	.0304	.0366	.0384	.....	.033
3	.....	.1902	.1809	.1777	.1741	.1946	.....	.207
Antennal joint 3, base to apex of basal sensorium	.....	.0562	.0634	.....	.0536	.0589	0.063	.....
Antennal joint 3, length of basal sensorium	.....	.0268	.0304	.0241	.0214	.0304	.0275	.....
Antennal joint 3, length of apical sensorium	.....	.0286	.0269	.....	.0250	.0277	.0297	.....
Hind femur, length	.....	.1901	.1802	.1500	.1848	.....	.....	.....
Hind tibia, length	.....	.2179	.2250	.1643	.2062	.....	.....	.....
Beak, length	.....	.....	.....	.....	.229	.....	.....	.....
Wing expanse	.....	.....	.....	.....	.....	.....	2.73	.....

The prenymphal instar is passed in three or four days, in the same time in which the corresponding instar of the wingless radicicole is passed. The nymphal instar, however, is relatively longer than the corresponding instar in the wingless form, and it is because of this fact that the migrant takes longer to mature than does the contemporaneous wingless radicicole. The nymphal or pupal instar occupies from 5 to 12 days, the average being about 8 days.

The nymphs take more food than does the corresponding wingless form, and after they have left a nodosity or tuberosity upon which they have been feeding, the lesion rapidly decays unless other individuals are settled upon it. The nymphs do not usually move much during their period of growth, but if disturbed they move quickly and display a negative phototropism when suddenly exposed to light. The newly molted nymphs, however, often wander about with apparent aimlessness. The full-grown nymphs just before molting ascend the roots, seeking the surface, and transform on the trunk or else find their way along the root until they come to a crack in the soil, and crawling up the sides of the crack transform near the surface. In glass sections cages, wherein the glass plates did not fit very tightly to the soil, the nymphs were found sometimes crawling up to within 2 or 3 inches of the surface and sometimes transforming close by the roots as much as 17 inches below the soil surface, the resultant winged aphids being compelled to find their way to the surface. It was concluded that owing to the loosely fitted glass plates of the section cages, which allowed abnormal light to penetrate below the surface of the soil, the nymphs did not wait to ascend toward the surface, but transformed below, their transformation being governed by the strength of the light rays to which they were subjected. It may be said that these section cages measured 9 by 24 inches, outside measurement, and allowed of a thickness of half an

inch of soil, which was a silty loam mixed with heavier clay loam. In some half-darkened cages, containing potted vines, the nymphs were observed to ascend to the level of the soil surface to transform. On the other hand, occasional nymphs have been found to transform on the roots as much as several feet underground, and many of the resultant migrants failed to reach the surface of the soil.

HABITS OF WINGED MIGRANTS.

Occasionally it was noticed in the jars that migrants would thrust their beaks into the roots and appear to feed. While engaged thus they lower the head so as to allow the beak to penetrate the tissues of the root. This organ appears to issue from the mesosternum, because of the curvature of the sheath. The femora are kept horizontal, and the antennæ are usually in motion. While the insect is walking the antennæ are in motion. The migrants, so far as has been noted, never feed after they issue from the soil. At all times they exhibit strong positive phototropism. When placed in a room they seek to crawl toward windows, and their activity is greatly increased when placed in the direct sunlight. If placed in a petri dish in the sunlight, they travel very fast and often take to flight, and are capable of keeping up a walking gait for hours. If the surface upon which they are standing becomes heated, they quickly die. If a vine leaf or other shade-giving object is placed in the dish, the phylloxeræ will finally settle on the shady side of the object. In the vineyard most of the winged phylloxeræ were observed to issue from the soil by creeping up the stumps of the vine. On arriving at the surface many of them passed to the soil and crawled around aimlessly. Others crawled up the vine, and when they reached a point of vantage, such as the end of a cane, they spread and vibrated their wings, as though inviting the wind to bear them off. Finally they launched themselves into the air and if they struck a wind current were borne off. Often after spreading their wings once or twice they turned about and crawled down the stalk, and frequently when they launched themselves into the air no current of wind caught them, and they half fell and half flew to the ground in an oblique direction, but at other times they flew off strongly without the aid of the wind. The migrants are capable of traveling by flight and with the wind, as is evidenced by the experiments conducted with sticky papers. (See Diffusion of phylloxera, p. 100.) They have been taken on such papers at least 80 feet from the nearest infested vine, and undoubtedly they may travel much farther.

In order to ascertain whether the migrants returned to the soil by crawling down the stem of the vine, 26 migrants were placed on the upper foliage of a small American vine (9 inches in height), on

August 17, 1914. Around the base of the vine stem were placed sticky papers, and the stem was encircled with glue. The vine was kept indoors and was not exposed to wind currents. Six hours after the phylloxeræ were placed on the leaves, eight individuals were caught on the paper. After 24 hours, 17 winged phylloxeræ were on the paper and 3 dead on the leaves, none having been caught in the circle of glue on the stem. Thus the phylloxeræ had either flown or dropped down and none had descended the full length of the stalk. Since none of the individuals on the papers were over 4 inches from the stem it would appear that they dropped rather than flew from the vine.

On August 22, 1914, 34 winged phylloxeræ were placed on the foliage of a riparia vine, 12 inches in height. This vine was potted and sunk in the soil and exposed to field conditions. Around the base an area of sticky paper 30 by 36 inches was laid. After two days an examination of the paper showed on the leeward side eight winged phylloxeræ, occurring 16½, 16½, 16, 16, 12, 10, 6, and 1½ inches, respectively, from the stem, and one winged phylloxera on the windward side 2 inches from the stem. The remaining 25 were not recovered, and probably flew off or were blown beyond the paper. The location in which this experiment took place was subjected to wind that blew from one direction only. It is obvious that the wind was a factor in the distribution of these phylloxeræ.

In the observations on the flying of the migrants it was found that individuals would fly both in the sunlight and in the shade, that very frequently they refused to launch themselves even in bright sunlight and in all varieties of wind currents, and that they appeared to take no definite direction in launching themselves. As a general rule, the winged forms fly more abundantly in the sunshine than in the shade, and they are the more active the hotter and drier are the conditions of their environment.

PRODUCTION AND RELATIVE ABUNDANCE OF MIGRANTS.

In 1911, in the course of rearing experiments conducted in the laboratory cellar, the first winged forms were secured on August 2. These had been raised on a heavily infested piece of vinifera root and were part of the third generation of that year. In five localities in central California nymphs were collected in vineyards from August 3 to 19 and, judging from observations made in years following, it is possible that nymphs had been developed earlier in that season. In the laboratory the production of migrants proceeded until the end of November, but in the latter half of October and in November only a few developed.

In 1912 no record was made of the earliest appearance of nymphs and migrants, but they were found abundantly on young potted

vines (mostly resistants and American nonresistants) during September and October, and some were reared in the cellar during August.

In 1913 the first nymph was observed, July 9, on the root of an American vine, and at about the same time others appeared on young resistant hybrids in pots. On the severed pieces of vinifera roots kept in jars in the cellar nymphs occurred as early as July 12, and on July 17 the first migrants appeared. This was the first year in which experiments were conducted with living vines in cages, and on these the earliest nymphs and migrants were reared on July 20 and 28, respectively. In the experimental vineyard (Zinfandel) migrants were first collected about August 1, but some nymphs were found on July 25 in a vineyard at Napa, Calif. In general, migrants continued to develop until November, but after the middle of October their production was scanty, and in the vineyard very few were found later than September.

In 1914 nymphs were first observed on June 16, both in the experimental vineyard at Walnut Creek and on roots kept in the cellar. On June 18 a migrant was reared from a nymph collected in the vineyard two days previously. On the roots of the vines growing in cages nymphs were reared June 23. Throughout July and August nymphs and migrants were abundant in the Zinfandel vineyard. In September the numbers fell off rapidly and none were found in October. In infested vines in pots migrants were secured in considerable numbers throughout August and September, but were much more scarce in October.

In 1915, in the material reared under cellar conditions, the first nymph was observed on June 14. The day following, a nymph occurred on the root of a young vine planted in a section cage. In the cages containing living vines, the first nymph was reared June 23, and in the experimental Zinfandel vineyard, nymphs were collected June 22 and evidently occurred as early as June 15. In the vineyard the production of migrants continued until the end of September, and was abundant from July 15 to the end of August. In the material in the cellar jars, abundant migrants were secured throughout the months of July, August, and September, and the production continued until November 8.

In summing up, it may be said that in California the period in which migrants are developed in vineyards extends from the middle of June until the end of October; that these forms appear in greatest abundance from the middle of July to the middle of September (the hottest time of the year); and that the production is very limited in June and October. In small vines in pots, especially if consistent irrigation is practiced, the October production of migrants

was frequently large. In the case of pieces of vine roots kept in a cellar, abnormal conditions of food, temperature, and humidity frequently arose.

The conditions which affect the relative abundance of migrants are the following: Variety of vine, vigor of vine, humidity, temperature, condition of roots, character of soil.

Resistant and certain American nonresistant vines normally bear the greatest proportion of migrants. These vines are the descendants of the wild grapevines which formed, and still form, the natural food plant of the phylloxera, and which were immune from serious injury by reason of the fact that there was produced each year a large percentage of migrants, while few or no wingless forms persisted on the vines after the winged forms had departed. The wingless radicicole forms during the summer fed only upon the terminal rootlets, and when these decayed the vine was easily able to replace them without suffering injury of any consequence. The resistant vines of to-day, except in instances in which the roots have been supplied with poor or insufficient soil, as is noted below, do not support heavy and continued infestations of wingless phylloxera, and almost all the phylloxeræ born in summer and autumn develop wings and become migrants. It may be said here that experimenting with resistant vines grown in pots with soil unchanged for over a year is apt to give misleading results, for as the soil becomes poorer and insufficient for the increasing root system of the vine, fibrous rootlets become scarce, and an abnormal infestation of wingless phylloxeræ and a diminishing production of migrant phylloxeræ ensue, thus approaching the conditions normally found on vinifera vines. On vinifera vines and on many American nonresistants, such as Isabella, Catawba, and Champion, the production of winged migrants is never proportionately as large as that which occurs on resistants. Well-nourished resistant vines have been observed to rid themselves entirely of the phylloxeræ, the insects all departing as winged forms, and in all cases under normal conditions, if any wingless forms remain after the winged forms have all left, the number is very small. On vinifera vines the total nymphal production has been found to be over 33 per cent of the whole in season, although three-fourths of the individuals produced on fleshy surface rootlets and on nodosities have been observed to develop into migrants, and on succulent pieces of severed root cuttings as large a proportion has been reared.

In the vineyard the larger roots were rarely found to produce a number of migrants in excess of 25 per cent of the whole number of phylloxeræ simultaneously developed, and under unfavorable conditions extremely few and sometimes no migrants were produced.

Under average conditions the proportion on the larger roots was between 5 and 10 per cent. Regarding the American vines of nonresistant type, a considerable diversity in the production of nymphs has been observed. On some, like Moore's Early, this production may be proportionately very large, while on others, like Isabella and Catawba, it may be smaller than on viniferæ, as occurred in the experiments in caged and potted vines. Vines like Agawam, Lenoir, and Delaware, vinifera crosses, bore about the same proportion of nymphs as the viniferæ, but among the labrusca types (Isabella, Moore's Early, Concord, Champion) there was considerable variation.

On resistant vines, the nymphs are developed on the nodosities, but on viniferæ and American vines of nonresistant type they are also produced on other portions of the root system. On phylloxerated viniferæ, the most abundant production of nymphs occurs on the fleshy and fibrous surface rootlets frequently observable in the vineyard. These rootlets are sent out in May and June, and often become grossly infested with phylloxeræ in June and July. Toward the end of July, they decay or dry out, and after that nymphs are produced only on the larger roots and on nodosities deeper in the soil. On the larger roots relatively few nymphs are produced before August or after September.

Among viniferæ the more vigorous vines produce the greater proportionate numbers of winged forms. Badly stunted vines showing several years of phylloxeration produce comparatively few, while the recently attacked vines around the periphery of "spots" produce large quantities. Viniferæ vines in pots produce great numbers the first year of infestation, but if the soil is unchanged in the second and third years, as the vines become weakened, they produce fewer winged forms.

As far as has been observed, all varieties of viniferæ produce the same proportion of migrants.

It has been observed frequently that a humid environment stimulates the production of migrants and a dry one precludes it. This has been especially noticeable in the cases of young vines in pots and of the severed roots kept under cellar conditions. The late appearance of the migrants in the experimental vineyard in 1913 as compared with those of 1914 and 1915 was perhaps due to lack of moisture in the soil in summer. The spring of 1913 was exceptionally dry, and the ground became very dry by June, whereas in the two years following, moisture was conserved in the top soil until July. The total migrant development of 1913, however, although at first retarded, was finally just about as large as those of the succeeding years. To hold the severed pieces of roots, glass jars and dishes were used in the cellar, and it was found that in the summer and fall

a layer of wet sand placed in the bottom of the jar was conducive to the production of migrants. When moisture was applied periodically to filter papers, the production of migrants was greater the more frequent the applications.

What effect, if any, temperature has upon the production of migrants can not be shown except that they are produced during the hottest months of the year. Contrasting the hot summer of 1913 with the cooler one of 1914, it was found that the production was about equal each year.

Migrants are produced in greater numbers in soils which retain moisture than in those which dry out rapidly. Otherwise no further influence traceable to soil conditions has been noticed. Although the general behavior of phylloxera differs considerably in relation to different types of soil, as between these different types the production of migrants does not appear to change.

In the season 1914, 12 vinifera vines were growing in cages. These were inoculated in the spring, and six of them later treated throughout the summer and autumn with fertilizers applied in liquid form periodically. These fertilizers—nitrogen, potash, phosphoric acid, and magnesium—were combined in a normal fertilizer and also used in combinations in which one element was in marked excess. The fertilized vines produced noticeably larger nymphal infestations. In 1915 other potted vines were treated likewise, except that all the fertilizer was mixed with the soil at the time of planting, and the vines were not inoculated until a month later. In this series the number of nymphs was no greater or less on the fertilized vines than on the unfertilized.

Migrants formed part of radicicole generations 2 to 5, those of the third generation being the most abundant. It was never observed that any of the first generation (direct progeny of the hibernants) became winged.

NYMPHICALS OR INTERMEDIATE FORMS.

The insects of the nymphical type are intermediate in form between the winged migrant and the wingless radicicole. In their adult stage they vary largely. Grassi (11) has figured and described several individuals which represent stages in the variation. His specimens varied from a type which differed only from the radicicole in the possession of two or three extra eye facets and in longer appendages to one which superficially resembled a nymph in that it had well-developed compound eyes and noticeable wing pads. This last type, however, upon close examination, differed from the nymph as follows: (1)The antennæ (fig. 8; compare with fig. 9, antenna of nymph) frequently bore two sensoria, as in the winged insect, but the basal sensorium was less developed than in that form; (2) the wing pads

were not hard and straight and parallel to the sides of the body, but bulged out and appeared rolled up and were soft, also sometimes containing the sensory organs peculiar to the wing of the winged forms; (3) there were no wing muscles in the interior of the thorax; and (4) the structure of the vaginal segment of the abdomen was more developed than in the nymph. From this it appeared that this type of nymphical was more comparable to the winged insect notwithstanding its superficial resemblance to the nymph, and this conclusion would be the more obvious when it is considered that the nymphical is an adult insect of the fifth stage.

In Italy the intermediates are said to be quite abundant among the nymphs in the season of the year (July to October) when the latter are being produced on the vines. They were found to be especially abundant on vines of the American type but also not uncommon on viniferæ.

In California, in the year (1915) in which were carried on researches upon the intermediate forms, there was a very small available supply of infested American vines, and the observations were confined chiefly to viniferæ. On the American vines such as were examined one nymphical was found.

In looking over a series of slides made in 1914, a single nymphical was recognized; the year following, during the nymphal season (June to November), frequent examinations were made on vinifera vines, and in all 15 intermediates were secured from these. The individual from the American vine (Wyoming Red) and nine of those on viniferæ were recognized through the medium of mounting large numbers of insects and later examining them through the microscope. The remaining six were discovered on the roots through the use of a binocular microscope, and all of them had rudimentary wing pads, so that it is likely that others of the type lacking these pads were observed but not recognized as intermediates.

In the two years covering the investigation a total of 17 intermediates came under observation. None of these was found earlier in the year than the middle of September, and 12 were collected or observed between September 14 and 27, 1915, and 1 on September 10, 1914. Of the 4 remaining, 1 was observed on a piece of root October 14, 1915, and 3 others October 27, 1915, 1 of which was in the fourth stage and matured November 1. These 17 individuals differed greatly one from another and represented all the types discussed by Grassi and Foa. The types intergrade, and, in fact, no two of the examples were alike. For the sake of comparison, they may be divided into three arbitrary groups: (1) Those without vestige of wing pads; (2) those with small buttonlike wing pads not visible from above; (3) those with larger wing pads protruding (as in the nymphs, fig. 9) beyond the lateral margin of the body and there-

fore visible from above. In group 1 were two individuals collected on young vinifera vines. One of them greatly resembled an adult wingless radicicole, but besides the larval eyes it had two to three extra facets, and the antennæ and legs were longer than in the radicicole. The other was slender, resembling a prenymph in shape, and had about six extra eye facets, and one antenna showed two sensoria. Group 2 (fig. 6) had six representatives, all with small to very small rudimentary wing pads invisible from above. In all cases the antennæ (fig. 8) and legs were long, and one insect had two sensoria on antennal segment III. In shape the individuals resembled wingless radicicoles. One specimen (from Wyoming Red) had no extra eye facets, and the others from young viniferæ had a varying number, usually 10, although one had about 15. The remaining 9 individuals came under group 3 (fig. 7), and, because of their more pronounced nymphlike characters, these are more easily observed in life upon roots than are those of the other two groups, and 4 of the 6 individuals recognized alive on roots were of this type.

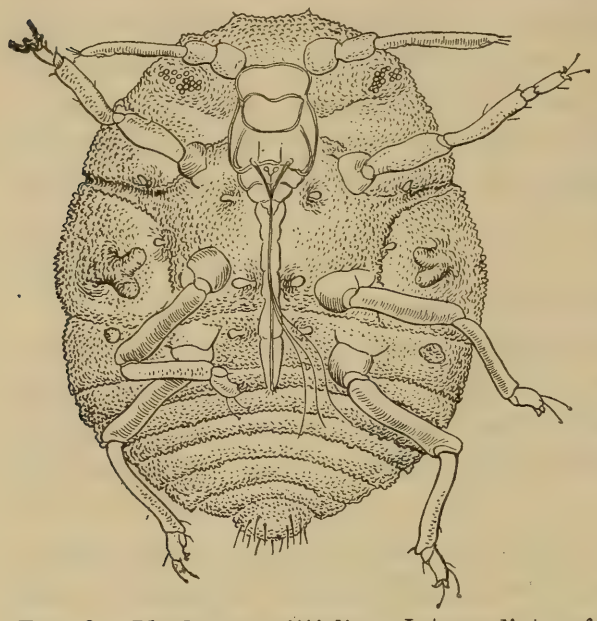


FIG. 6.—*Phylloxera vitifoliae:* Intermediate of type 2, ventral view. Much enlarged.

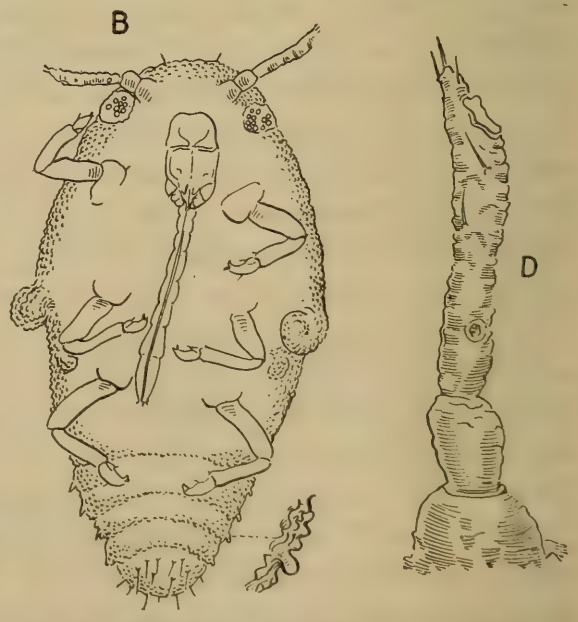


FIG. 7.—*Phylloxera vitifoliae:* Intermediate of type 3, ventral view, much enlarged; antenna at right, more enlarged.

It is probable, judging from random collections, that the insects of groups 2 and 3 are about equally abundant and each somewhat more so than those of group 1. All the individuals of group 3 had rudimentary wing pads, in many cases almost as large as the wing pads of the nymphs. They bulged out from the sides of the insects, and were soft and appeared coiled (fig. 7) or curled. The compound eyes were well developed, there being from 66 to 100 per cent as many facets as in the nymphal eyes. In some cases the larval

eyes were absent, and in no case were ocelli discernible. In most individuals there were two sensoria on the last antennal joint, and in one antenna there were two small basal sensoria and the usual apical sensorium, making three in all. The basal sensoria were not in any case as large as those of the winged migrant. The antennæ and legs were about as long as those of the nymph, noticeably longer on the average than those of the individuals of group 2, which in turn were longer than those of the two individuals of group 1.[10] It would appear, therefore, that greater development of wing pads and compound eyes is complemented with a lengthening of legs and antennæ and a tendency to bear the extra sensorium of the winged forms. The femora exceed the tibiæ in length.

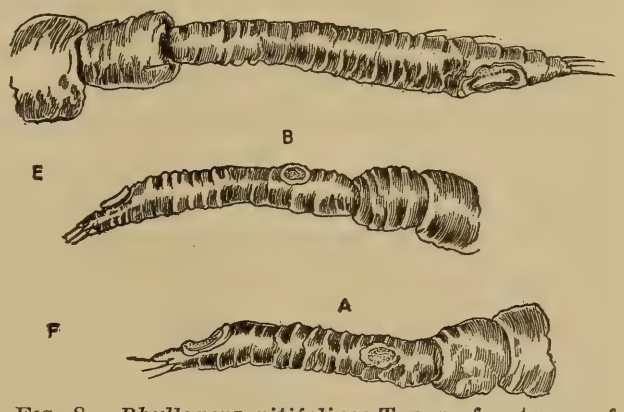


FIG. 8.—*Phylloxera vitifoliae:* Types of antennæ of intermediates. Greatly enlarged.

There is among the intermediates a tendency toward asymmetry. This was remarked in Italy and has also appeared in California. One eye may have more facets than the other; the lengths of antennæ and legs may differ in individuals, those of one side being longer than their counterparts, and one antenna may possess more sensoria than the other.

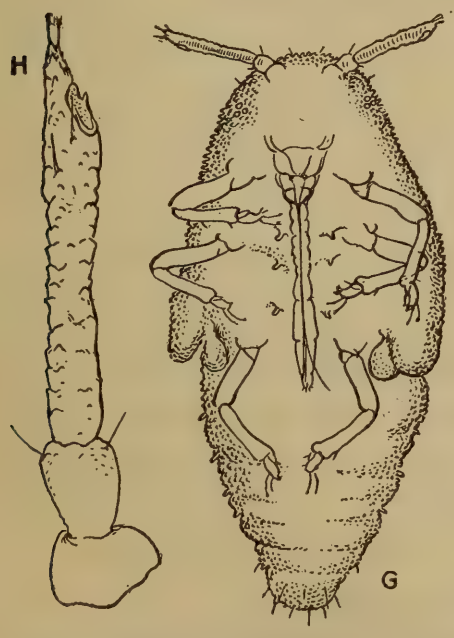


FIG. 9.—*Phylloxera vitifoliae:* Nymph and antenna of newly molted insect, for comparison with intermediates.

In two instances the fourth stage of intermediates was observed in California. In one case an individual of group 3 molted from what appeared, under the lenses of the binocular microscope, to be a true nymph. In the other case an example of the same group molted from an insect which itself resembled a nymphical; in fact, after the molt the individual did not appear to have changed its structure at all. In both fourth and fifth instars the wing pads were large and "fleshy."

From three individuals, all of group 3, eggs were obtained. These eggs could not be differentiated from eggs laid by wingless radicicoles. One nymphical deposited two eggs, which were lost. An-

[10] The insect depicted in figure 7 is considerably less enlarged than that represented in figure 6.

other deposited two eggs, on September 28 and 29, respectively. These hatched in 11 days, the resultant larvæ obviously being radicicoles but surviving only a few days. The third individual matured November 1, and between this date and November 10 it deposited 10 eggs. After this it became weak, and on November 16 was mounted on a slide. The eggs were exactly similar to those laid by wingless radicicoles, and two of them measured, respectively, 0.310 by 0.166 mm. and 0.297 by 0.168 mm. Seven eggs were transferred for observation to another root, and three eggs hatched in from 14 to 16 days, the resultant larvæ settling down for hibernation. One of these soon died, but the other two passed the winter in due form, and matured in April, 1916. Both of them were typical radicicoles and subsequently deposited many eggs.

In Italy Grassi and his assistants found that the great majority of the intermediates were parthenogenetic, but one individual was found to contain a sexed egg. In discussing the phenomenon of the intermediates, they gave it as their opinion that the parthenogenetic individuals were those which up to their third stage were destined to become radicicoles, but in that stage changed their development to that of winged migrants, while the character of their eggs had been already fixed before the change and so remained parthenogenetic. In the case of sexuparous intermediates the change was made in the reverse direction, the larvæ at first being destined to become migrants and, therefore, when they matured as nymphicals they deposited sexed eggs.

In California the recorded eggs laid by nymphicals were all parthenogenetic, but the possibility of some of such eggs being sexual is not entirely excluded, in the writers' opinion.

The nymphicals do not leave the roots in the manner of the winged insects, and therefore deposit their ova on the roots. In the case of sexuparous nymphicals, the sexes and winter egg would presumably develop underground. Whether in California such a development occurs or not can not be stated from our present knowledge, but in view of the fact that for many years the leaf galls have been unknown, it appears certain that such a cycle proceeds no further than the winter egg.

DEPOSITION OF THE SEXUAL EGGS.

The migrants deposit eggs (Pl. VIII, *f*, *h*, *i*) which are of two kinds, viz, male and female, and from these eggs issue the true sexual aphids. Sexual eggs have never been found by the writers in the vineyard, either on viniferæ or on resistant vines, although a large number of vines have been examined. In laboratory experiments a large number of sexed eggs have been produced. Considerable discussion has taken place among European writers as to the normal

location of the sexed eggs. Taking the sum of these discussions, it appears that they are placed on the underside of the leaves and more abundantly in the bark, generally between the year-old layer and that of the current year, and are fastened to the inner side of the former. Occasionally eggs are found at the base of canes where the new wood joins the old, and rarely on the vine supports (stakes). They are laid on both viniferæ and resistant vines, but preferably on the latter.

Observations were conducted in small cages, and in a few instances on living vines in pots. In the latter instances eggs were found laid on both the foliage and bark. Many different kinds of cages were used and experiments with different degrees of light, moisture, and temperature were conducted. Vine leaves and pieces of bark were inclosed in the cages. As a rule, the migrants, though primarily attracted to light, deposited their eggs in semidarkness. They laid them on the leaves and more rarely on pieces of bark offered, but often also on the sides, lid, and floor of the cages and in cracks. In 1911 the observations tabulated in Table XXVII occurred.

TABLE XXVII.—*Sexual production of the grape phylloxera, Walnut Creek, Calif., 1911.*

Number of migrants.	Date and location of migrants.	Number of sexual eggs deposited.[1]	Date of deposition.	Date of maturing of sexes.	Number of sexes matured.[2]
25	Aug. 4–6: Riparia vine in pot	16	Aug. 9	.....	.....
52	Aug. 7–8: Vinifera vine in pot	0	.....	.....	.....
65	Aug. 10–12: Riparia vine in pot	18	Aug. 16	Aug. 26	4
				Aug. 28	1
80	Aug. 13, 14: Vinifera vine in pot	2	Aug. 15	Aug. 30	1
		1	Aug. 20	.....	0
25	Aug. 15: Riparia vine in pot	2	...do.....	.....	0
36	Aug. 16: Riparia vine in pot	5	...do.....	.....	0
30	Aug. 17: Glass tube in drawer	0	.....	.....	.....
83	Aug. 18, 19: Riparia leaves in petri dish	7	Aug. 21	Sept. 6	1
		5	Aug. 22	.....	0
		12	Aug. 23	.....	0
1	Aug. 19: Leaves in petri dish	1	Aug. 19	Aug. 30	1
?	Aug. 23: Leaves in petri dish	7	Aug. 23	Sept. 2	1
69	Aug. 24: Riparia leaves in laboratory	1	Aug. 25	.....	0
		1	Aug. 26	.....	0
		1	Aug. 27	.....	0
		8	Aug. 28	.....	0
		1	Aug. 29	.....	0
30	Aug. 25, 26: Riparia leaves in petri dish	1	Aug. 27	.....	0
		6	Aug. 28	.....	0
		1	Aug. 30	.....	0
45	Aug. 25, 28, 29: Riparia leaves in petri dish	7	Sept. 3	.....	0
103	Sept. 2–17: Vinifera vine in pot	30	Sept. 25	Oct. 4	1
				Oct. 5	1
				Oct. 6	2
50	Sept. 19–23: Riparia vine in pot	6	Sept. 29	.....	0
40	Sept. 25–29: Riparia vine in pot	0	.....	.....	.....

[1] Thirteen female and three male eggs.
[2] All maturing sexuals were females.

TABLE XXVIII.—*Summary of Table XXVII.*

Number of migrants	734
Number of sexual eggs deposited	171
Number of sexual eggs hatched	13

Individual egg deposition by migrants, recorded for 5 individuals, was as follows: 3, 2, 1, 4, and 3; average, 2.6. Obviously the great majority of migrants died without depositing eggs. The eggs above recorded were laid in from 2 to 9 days, the majority in from 3 to 5 days, after the migrants emerged from the nymphal skin. The great majority of the migrants did not live more than 3 days after casting their final molt, confinement evidently having caused premature death.

From 100 migrants produced August 15, 1912, and placed on a small vine August 20, a single egg, which failed to develop, was deposited August 24.

In 1913 different types of cages were utilized in an effort to induce a larger percentage of eggs and mature sexuals. The results were not encouraging. From July 17 to October 17 migrants were placed in the cages. During that time in some 60 experiments, 317 migrants were used, 99 sexual eggs were secured, and 7 sexed phylloxeræ (all females) matured. The migrants in no case lived more than 6 days, the majority only 3 days, and quite a number did not move their position after having been placed in the cages. In most cases eggs were laid singly, but there was one group of 5, three groups of 4, and several of 3 and 2, laid by single phylloxeræ. In two cases eggs, presumably of separate sexes, were deposited in the same group by the same individual, but in all other cases it appeared certain that the eggs laid by individual migrants were of only the one sex. Judging from the size, about twice as many female as male eggs were laid, besides quite a number (about 20 per cent) of eggs of an intermediate size. No male or intermediate sized eggs hatched, but it was noticed that the male eggs, as they developed, assumed a darker color than did those of the female. After a certain point in the development, all the moribund eggs began noticeably to shrink and turn dark brown. None of the eggs showed signs of infertility, and within about five days of deposition hatching occurred and the eyes and body segmentation were visible, after which the moribund individuals discolored and shrank rapidly. Dead migrants were found occasionally on the roots and sides of the cellar jars, beside eggs that they had deposited. In the vineyard such a procedure was never observed, and therefore it is believed to be quite abnormal, and probably results from the inability of the migrant to escape from the cellar jar after having been overlooked in the periodical examinations for migrants.

During the summer of 1914 a further series of experiments on the production of sexual eggs took place. The temperature that year was considerably below that obtaining in the years 1911 and 1913, and this may account for the lack of sexuals maturing. In 1914 the cages utilized in 1913 and some of other types were employed.

The experiments began June 27 and terminated September 7. Three hundred and ninety-seven migrants produced a total of 143 eggs from which no sexual forms developed. Thus the proportion of deposited eggs to migrants in 1913 was 1 to 3.2, while in 1914 it was 1 to 2.75, and in 1911, 1 to 4.3. In 1914 four migrants each deposited four eggs, and three eggs were deposited in nine instances, but most of the eggs were laid singly. In no case could it be definitely said that eggs of more than one sex occurred in individual groups. About three times as many female eggs as male were deposited, and about one-fourth of the eggs were intermediate in size (probably males). The winged sexuparæ died on the average two and one-half days after they were admitted to the cages, or about four days after they had transformed from the nymphal instar.

In 1915 experiments were continued, migrants being secured from June 26 to October 27. Part of these were used in stender and petri dishes, part in small circular rubber cells ($\frac{3}{16}$ inch high, $1\frac{1}{4}$ inches in diameter) mounted on microscope slides with cover glasses for lids, and a few on a living vine (Riparia). In the dishes small pieces of vine, bark, or leaves were placed, leaves of the Champini being used mostly on account of the fact that the migrants prefer to deposit eggs on a tomentous leaf. The effect of variations in temperature and humidity was noted.

A total of 1,961 migrants deposited in all 472 eggs, and 52 sexuals matured. Thus the proportion of eggs to migrants was approximately 1 to 4.15. In the stender and petri dishes and on the living vine combined, 938 migrants deposited 167 eggs, a proportion of 5.6 to 1, of which 16 sexuals matured. In the rubber cells mounted on microscope slides, 1,023 migrants deposited 305 eggs, a proportion of 3.3 to 1, and 36 sexed forms matured. The rubber cells therefore gave a greater proportion of eggs per migrant. Part of these cells were kept in a cellar and part inside a slide box in a room of the laboratory. The egg deposition was not appreciably different in these two situations, but the sexes under the almost constant temperatures of the cellar matured better than under the fluctuating temperatures of the room. Part of the dishes also were kept in the cellar and part exposed to light in the room. Those in the latter situation averaged more eggs per migrant, but the proportion of sexes which subsequently matured was similar to that of the migrants and dissimilar to that of the eggs.

It appeared at first that exposure to light induced the migrants to deposit a greater proportion of eggs and later appeared to have prevented a large proportion from maturing. Judging from the fact that the amount of light to which these eggs were subjected during their development was not greater than occurs under natural conditions, however, it would appear that this supposition is incor-

rect and that the disproportionate mortality among the eggs was caused rather by the uneven temperatures prevailing in the room. The presence or absence of humidity had no apparent effect on the deposition of eggs. Eggs and sexed forms developed better in dry than in moist rubber cells, but in the dishes exposed to light the converse occurred. Part of the migrants were stimulated to fly in the sunshine before being placed in the cages, and deposited a somewhat larger average number of eggs than those which had not flown, but the flight or nonflight of the migrants did not appear to influence the subsequent development of the eggs and sexes. In July and the first half of August, when the temperatures reached a maximum, there was a higher average in egg production and in the proportion of sexuals matured, yet during the period September 16 to October 27, despite lower temperatures, a larger average proportion of eggs per migrant and of mature sexes was produced than during the intermediate period from August 16 to September 15.

On the whole, development was most successful where migrants had flown and when eggs were kept in moderate light and in a moderately humid environment.

The longevity of the migrants, the number of eggs deposited per individual, and the proportion of male and female eggs laid coincided with the results of experiments in 1914.

It is only necessary to consider the very small proportion of eggs laid per migrant (in 1915, for instance, 1 to 4.15) and the very small proportion of eggs which succeeded in developing into mature sexes (in 1915, 1 in every 9) under artificial conditions to realize how abnormal these conditions must have been. From observations made in California during 1915 the complement of migrant eggs was found to average 2.6, so that if all the migrants in the experiments in that year had deposited their full complement, ten times as many eggs as were actually deposited would have been obtained. European experimenters have had, for the most part, similar results in their study of migrants in confinement.

In not a single instance was a migrant observed to deposit other than a sexual egg, so the possibility of the occurrence in California of a parthenoparous winged form may be regarded as excluded. There occurs, however, a parthenoparous nymphical form, which has been discussed above (p. 82).

THE SEXUAL FORMS.

The sexual forms (Pl. VIII, *j–m*), male and female, issue from eggs deposited by the winged sexuparæ or migrants. These eggs are of two types, male (Pl. VIII, *f*) and female (Pl. VIII, *h*, *i*). Writers have attempted to recognize a third type intermediate in size

between the larger female and the smaller male egg, but these intermediate eggs are apparently always of the male sex. Thus there is a considerable variation in the dimensions of the male eggs, as, indeed, there is in those of the mature male insects. According to Grassi (11, p. 134–135) eggs producing females vary in length from 0.384 to 0.323 mm., and in width from 0.176 to 0.164 mm.; eggs producing males, in length from 0.247 to 0.250 mm., and in width from 0.152 to 0.134 mm. He also states that eggs of the intermediate dimensions are fertile and are of the male sex, and that male and female eggs may exceed the limits in one dimension, but never in two. On the average the female eggs were slightly larger than the radicicole eggs and the male eggs slightly smaller, but intermediate eggs had measurements identical with those of the radicicoles.

Measurements of sexual eggs, made in California in 1913, indicated a range in length from 0.450 to 0.257 mm., and in width from 0.171 to 0.117 mm. A single female of these hatched (0.357 by 0.171 mm.). In the light of measurements made in 1914 and 1915 it appeared that eggs of the sexes were similar in dimensions to those recorded by Grassi for Italy, except that the range in sizes was somewhat greater.

The sexual eggs are bright shining yellow. The eggshell is very thin and membranous, quite differently formed from that of the radicicole. The egg hatches after about four or five days' incubation, the process of hatching consisting in the sloughing off of the thin shell, the emerging aphid settling at the place of hatching. The eyes and body segmentation become visible, and the undeveloped appendages are carried under the body. The insect then undergoes four successive molts, and does not move away until it is mature. During the first three instars there appears but little change, except that the body segmentation becomes more distinct. After the third molt the appendages project slightly beyond the sides of the body, but otherwise no visible change occurs. All the molted skins are contained one within another, adhering to the posterior end of the body, and when the last molt has taken place the adult moves away, leaving the "nest" of telescoped skins and eggshell behind. It sometimes happens that the adult is unable to cast off this pad of skins. The mature sexuals are capable of running actively, and, according to European investigations, they may live for some weeks, thereby facilitating a meeting of the sexes. The sexuals take no nourishment. The female is slightly larger and the male slightly smaller than the newly hatched radicicole.

DESCRIPTION.

THE SEXUAL FEMALE.

Orange or orange yellow; antennæ and legs dusky grayish; antennæ longer than those of newly hatched radicicole. Body a little longer and wider than

the young radicicole. Caudal segment bluntly rounded. Eyes as in the radicicole larva. When the adult issues the single egg within is small, but within three days it becomes very evident (Pl. VIII, *j*) and occupies in section an area equal to about three-fourths of the entire insect.

TABLE XXIX.—*Measurements of mature sexual females of the grape phylloxera.*

	1	2
	Mm.	*Mm.*
Length of body	0.357	0.464
Maximum width of body	.200	.215
Length of "winter" egg contained	.313	.....
Maximum width of "winter" egg contained	.172	.....
Antennal joint 1, right, length	.017	.0200
Antennal joint 1, left, length	.016	.0179
Antennal joint 2, right, length	.013	.0205
Antennal joint 2, left, length	.013	.0188
Antennal joint 3, right, length	.054	.0580
Antennal joint 3, left, length	.053	.0553

THE MALE.

Dusky orange, darker than the sexed female; antennæ, legs, and genital segment dusky grayish; eyes of three facets each, red; beak absent. Body quite noticeably shorter, flatter, and narrower than that of the sexed female, and shorter and narrower than that of the newly hatched radicicole. Genital organ acutely conical.

TABLE XXX.—*Measurements of mature males of the grape phylloxera.*

	1	2
	Mm.	*Mm.*
Length of body	0.260	0.334
Maximum width of body	.094	.154
Antennal joint 1, length	.013	.....
Antennal joint 2, length	.018	.....
Antennal joint 3, length	.065	.071
Hind tibia, length	.046	.....
Hind femur, length	.056	.....

In confinement both sexes at first exhibit a positive phototropism, but after a day of maturity they seek shaded places. At first they are quite active, but later become sluggish. Undoubtedly they are much less active in confinement than in the natural state.

Table XXXI summarizes the development of the sexed form in the summer and fall of 1911 and 1913. All those which reached the adult state were females.

TABLE XXXI.—*Summarized record of sex development of the grape phylloxera, Walnut Creek, Calif., 1911 and 1913.*

	Number of individuals.	Days.
Average incubation period	12	5
Average postembryonic period	12	5.83
Average period of development	20	11.05

In 1915, in all, there were reared to maturity 52 sexuals, of which 9 were males, 2 of these having hatched from eggs of intermediate dimensions. These 2 males were noticeably larger than the other 7. The majority of the sexuals were reared in darkness under cellar conditions, the temperatures never averaging over 70.5° F. and in one instance falling to 61.5° F. A noticeable phenomenon was the death of a great number of sexes during the fourth instar, which appeared to be due to their inability to cast the final skin as a result of a deficiency of moisture. Tables XXXII and XXXIII show the development of the sexes in 1915.

TABLE XXXII.—*Development of sexed forms of the grape phylloxera, Walnut Creek, Calif., 1915.*

Individual No.	Date of egg deposition.	Date of maturing of sexual.	Developmental period.	Sex.	Average temperature.	Environment.
			Days.		°*F.*	
1	July 17	July 28	11	♀	70.3	Cellar.
2	...do	...do	11	♀	70.3	
3	...do	...do	11	♀	70.3	
4	...do	July 30	13	♀	70	
5	...do	...do	13	♀	70	
6	July 18	July 28	10	♀	.....	Room of laboratory.
7	July 22	Aug. 2	11	♀	70	Cellar.
8	...do	Aug. 3	12	♀	70	
9	...do	...do	12	♀	70	
10	July 30	Aug. 8	9	♀	.....	Room of laboratory.
11	July 31	Aug. 10	10	♀	69.8	Cellar.
12	...do	...do	10	♀	69.8	
13	Aug. 1	Aug. 12	11	♀	69.7	
14	...do	...do	11	♀	69.7	
15	...do	...do	11	♀	.....	Room of laboratory.
16	...do	...do	11	♀	.....	
17	...do	Aug. 13	12	♀	.....	
18	...do	Aug. 14	13	♀	.....	
19	Aug. 3	Aug. 12	9	♀	.....	
20	...do	Aug. 13	10	♂	.....	
21	...do	...do	10	♀	.....	
22	...do	...do	10	♀	.....	
23	...do	Aug. 14	11	♂	.....	
24	Aug. 4	Aug. 15	11	♀	69	
25	Aug. 5	Aug. 16	11	♂	68.8	
26	...do	...do	11	♀	68.8	
27	...do	...do	11	♀	68.8	
28	...do	...do	11	♀	68.8	
29	...do	...do	11	♀	68.8	
30	...do	...do	11	♀	68.8	
31	...do	...do	11	♀	68.8	
32	Aug. 6	Aug. 17	11	♀	68.5	
33	...do	Aug. 18	12	♂	68.5	
34	...do	...do	12	♀	68.5	Cellar.
35	...do	Aug. 19	13	♀	68.6	
36	Aug. 25	Sept. 8	14	♂	68.7	
37	...do	Sept. 9	15	♂	68.7	
38	Sept. 1	Sept. 15	14	♂	66.9	
39	Sept. 22	Oct. 4	12	♀	64.9	
40	Sept. 24	Oct. 9	15	♀	64.9	
41	...do	...do	15	♀	64.9	
42	...do	Oct. 10	16	♀	64.8	
43	Sept. 26	Oct. 12	16	♀	64.3	
44	...do	Oct. 13	17	♀	64.3	
45	Oct. 6	Oct. 21	15	♂	.....	Room of laboratory.
46	...do	...do	15	♀	.....	
47	...do	Oct. 22	16	♂	.....	
48	Oct. 7	Oct. 24	17	♀	62	Cellar.
49	...do	Oct. 25	18	♀	62	
50	Oct. 13	Nov. 1	19	♀	61.5	
51	...do	...do	19	♀	61.5	
52	...do	Nov. 3	21	♀	61.7	

TABLE XXXIII.—*Summary of Table XXXII.*

	Days.
Maximum developmental period	21
Minimum developmental period	9
Average developmental period	12.73
Average developmental period, female	12.65
Average developmental period, male	13.10

During the developmental period preceding September the sexes developed in an average of 11.1 days, and in the remaining period, from September 1 to November 3, in 16.1 days.

The males appeared to develop more slowly than the females, but a larger series might not indicate such a difference.

The sexes, as soon as mature, were confined in a microscope-slide cell with a piece of vine bark and some filter paper. None lived more than three days, and copulation was observed in several instances, but on the whole the sexuals showed little activity and were not much attracted to each other. Several of the females partly extruded a winter egg, but chose no especial locality for oviposition, and their action was undoubtedly abnormal.

Mating is said to occur normally on the bark of the vine, the female depositing a single egg under and between the layers of bark. The egg is attached by a curved peduncle generally to the inner surface of the 2-year-old bark, but sometimes to older layers.

The Italian investigators found that eggs were most abundant about midway between the base and head of the vine trunk, but that they might be deposited on any wood of 2 or more years of age as well as on buds. The egg at first is greenish yellow, and later becomes greenish brown, remaining so until the time for hatching in the spring following. The phylloxeræ issuing from the winter egg are said always to become the gallicole (gall-inhabiting) stem mothers.

At Walnut Creek all types of vines exposed to phylloxera infestation have been searched exhaustively without more than a single winter egg being found. Among these vines were included viniferæ taken from phylloxerated vineyards, and viniferæ and American experimental vines grown in pots and boxes. The single egg brought to light was observed in December, 1912, located under the outside layer of bark of a young potted vine (Champenal). This egg, after having been kept under observation for three weeks, died.

From all observations in California it appears that conditions are unfavorable for the successful development of the sexual phylloxeræ and, therefore, for the "winter" egg and succeeding generations of gallicoles. Since in some parts of France a similar condition in the phylloxera cycle obtains, it was concluded that some factor was lacking to insure successful development, and there was reason to believe that humidity was one of the factors until the discovery of

the existence of the gallicoles in Arizona under dry climatic conditions appeared to disprove this theory. At present it is held that the phylloxera in California is undergoing, and since it was first introduced (about 60 years ago) has continuously undergone, a marked change in habits resulting from variations in the character of its food. Wherever the phylloxera is attacking vinifera vines its habits are undergoing change. In many localities the production of sexuals, winter eggs, and gallicoles proceeds simultaneously with prolific agamous radicicole infestation, and in such places speedy diffusion of the species obtains by reason of the winged insects and gallicole in addition to the wanderers. In California and in certain other localities the spread of the phylloxera has been slow, primarily because the danger from the agencies of the migrants and gall inhabitants has been very slight, and this notwithstanding the presence of resistant vines, the type on which the gallicoles normally form the galls and on which the "winter" eggs develop the more successfully. Thus it appears that the phylloxera, since it has been in California, has modified its habits to suit its environment, by exchanging the complicated life cycle on its native plants (native vines of eastern North America) for the more simplified life cycle upon *Vitis vinifera.*

THE GALLICOLE AND ITS RELATION TO CALIFORNIA CONDITIONS.

In the eastern United States, in Arizona, and in the majority of the phylloxera districts in Europe the gall form or gallicole occurs. This is most prevalent in the more humid districts, and occurs chiefly on American vines and American hybrids and only rarely on *Vitis vinifera* and its hybrids. Recent research in European countries, especially in Italy by Grassi and his colleagues, has proved that the original gallicole hatches from the winter egg deposited during the previous autumn by the sexed female in a crevice in the bark. This larva hatches with the appearance of the first leaves and attaches itself to the surface of a young leaf, where its punctures produce a "pocket" formation in the leaf tissue. In this pocket it grows, matures, and deposits its eggs. Upon hatching, the resultant larvæ seek young leaves higher up on the growing cane, and, settling on the surface, cause further pocket formations. Succeeding generations follow throughout the summer, the numbers being more and more reduced by predacious enemies (Syrphidae, Agromyzidae, Coccinellidae, etc.), and also by a certain percentage of the newly hatched larvæ deserting the cane for the roots. Among the later generations the percentage of larvæ that seek subterranean existence increases, and such larvæ may be differentiated by certain characteristics, when newly hatched, from those destined to continue on the foliage. They possess relatively longer beaks and a different anten-

nal structure, including relatively larger sensoria. To these small larvæ has been given the name *neogallicolæ-radicicolæ* (young gall lice with root louse characteristics), while to the type which merely moves from one leaf to another younger one has been given the name *neogallicolæ-gallicolæ* (young gall lice with gall louse characteristics).

On the European vine (*Vitis vinifera*), according to Grassi, winter eggs were rarely laid and galls rarely found, the majority of those found being imperfect. It was apparent also that growth was much slower than on American vine foliage. In Italy, from eggs produced by nine gallicoles that had produced galls on a European vine, a few of the progeny had radicicole characteristics. This, however, was a rare occurrence, the great majority of young larvæ hatching in galls on European vines showing the gallicole characteristics and thus not being destined for subterranean life. The Italian investigators were able to cause radicicoles to settle and produce generations of gallicoles on the leaves of a Clinton (American) vine. This succeeded after several fruitless efforts. In this connection it may be said that, at Walnut Creek, on a small Golden Champion (American) vine, radicicoles ascending the stalk and ovipositing in crotches of the stem as high as 5 inches above the surface of the soil were observed in the fall of 1914. A few of the resulting larvæ settled still higher up on petioles. Finally cold weather in November ended this aerial infestation either by killing the larvæ or compelling them to descend below ground.

On July 16, 1913, a shipment of eight leaves of an American vine well infested with gallicoles was received from Vienna, Va. The gallicoles were egg-laying females, probably of the second generation (progeny of stem mothers), newly hatched larvæ, and large numbers of eggs. Only one adult occurred in each gall. Four of these leaves were placed contiguous to foliage of three resistant vines. The varieties were Riparia × Rupestris 3309, Columbaud × Riparia, and Solonis × Riparia. The first two named, small vines in pots, each were inoculated with one infested leaf; the third vine, larger and growing in the vineyard, was inoculated with two leaves. In no case were galls developed on the foliage of the three vines inoculated. It is to be recorded that these three vines were of a different type from the infested vine, but the Riparia type is susceptible to gallicole infestation.

On September 6, 1913, a selection of foliage of a Riparia hybrid infested with gallicoles was received from Washington, D. C. The following vines growing in the vineyard were inoculated with the infested foliage in close contiguity: Riparia × Rupestris 3309, Rupestris St. George, Rupestris × Berlandieri 301 A, Berlandieri × Riparia 34 E. M., Riparia × Cordifolia × Rupestris 111–8, Riparia

Gloire de Montpellier. The infested foliage had an abundant supply of newly hatched larvæ, but in no case did the inoculation succeed. It is possible, however, that many of the larvæ of such a late generation had radicicole characteristics, and therefore none such would settle on the leaves. Both of the foregoing series of inoculations were made under conditions of light atmospheric humidity. Recent research in Italy (11, p. 335–345) (17) shows that in that country, at least, humidity and irrigation have much influence in the production of galls on resistant vines. Both the Riparia × Rupestris 3309, and the Rupestris St. George are said by Panatelli to produce many galls in dry locations. It appears, however, that in general a greater humidity is conducive to the production of gallicoles on resistant vines and their hybrids. Thus out of 24 well-known resistant varieties enumerated by Panatelli, 21 produced many galls and 3 few galls in humid localities, while in dry locations 10 produced no galls, 5 few galls, and 9 many galls (17). In this connection, it may be added that in California resistant vines have been frequently observed growing among badly infested viniferæ and never showing any sign of gall infestation. On no occasion, indeed, have the writers ever observed phylloxera galls in California, and there is only one authenticated case in California of gallicoles, that being the discovery in August, 1884, by Dr. F. W. Morse (16), of gall-inhabiting phylloxeræ on a Canada (labrusca × riparia × vinifera) vine on the University of California grounds at Berkeley.

The two shipments of gallicoles cited above were also used in experiments to determine whether this form would live on roots. On July 16, 1913, 75 newly hatched gallicoles were placed on two pieces of severed root (Zinfandel) in a petri dish in the cellar. On a third smaller root 100 eggs from the galls were located. On August 18, on the two larger roots, five phylloxeræ with the typical radicicole characteristics matured. On September 3 there were altogether seven mature egg-laying radicicoles, of which six had matured on the two larger roots. Thus out of 100 eggs and 75 newly hatched larvæ only seven phylloxeræ matured.

On September 6 a similar experiment was begun on severed roots in the cellar. On two roots 75 eggs apiece were placed. These all turned black and none hatched, it appearing that the embryo suffered injury through fermentation that developed during the transcontinental journey. This supposed fermentation did not affect the larvæ already hatched and which were used for the foliage experiment.

A further experiment took place on roots of a living vine (Thompson's Seedless) which was inoculated July 16 with 50 eggs. Three insects from this inoculation matured August 12, 13, and 14. They were typical radicicoles and laid eggs at the rate of between two and

three daily, at first exceeding that number. These eggs were typical radicicole eggs, and produced further radicicole generations. Twelve of the eggs laid August 21–24 were transferred to another root of the same vine (Thompson's Seedless) and four insects matured between September 28 and October 5, after an average egg stage of about seven and one-half days and an average growing period of 35 days. The progeny of these four became hibernants, several of which matured and oviposited the following spring. These experiments demonstrate that under California conditions it is possible for larvæ hatching in galls to mature on the roots and become typical radicicoles. No observations were noted regarding the characteristics of the newly hatched gallicoles used in the experiments. After the inoculation, July 16, of 50 eggs on the root of the living vine it was seen that most of these eggs turned dark brown and failed to hatch. The observations on the hatching of this batch of eggs indicate that those failing to hatch were the earliest deposited, and it may be that the change in conditions and environment affected the embryonic development adversely.

The present nonappearance in California of the gallicole and its work on the foliage of grapevines, a condition paralleled in certain portions of Europe, vitally affects the entire biology of the insect, since it has been ascertained that the phylloxera issuing from the winter egg can only exist on the leaf or petiole as a gallicole. The Italian investigators Grassi, Topi, Grandori, and Foa found that no larvæ hatching from winter eggs fastened on the roots and that all of this generation of stem mothers (fundatrices) had the gallicole characteristics. This is a very important biological point. It is borne out by observations in those parts of Europe where the gall form is absent and in which winter eggs are extremely rare. It is similarly borne out in the phylloxera regions of California, where similar conditions occur. During the winters of 1912–13 and 1913–14, an extensive series of vines, large and small, of all types, many of which had been infested the previous summer with winged phylloxeræ, and others which, while themselves uninfested, had been growing near such infested vines, were examined. With only one exception, no trace of winter eggs or dead sexuals was found. This exception consisted in the single winter egg noted under the preceding heading.

EFFECTS OF WATER AND HEAT ON PHYLLOXERA.

Experiments were carried out to determine (1) the resistance of hibernant larvæ and eggs to water heated to various temperatures, (2) the resistance of hibernant larvæ to submersion in water at ordinary temperatures, and (3) the resistance of eggs to the heat of the sun.

During the winter of 1913–14, two experiments were made on the resistance of hibernants to hot water. The temperatures used ranged from 116° to 137° F., and the duration of submergence ranged from one to four minutes. A temperature of 120° F. failed to destroy the aphids completely, while 125° F. with a submergence of one minute destroyed all the insects. Similar treatment of the roots of living vines resulted in no appreciable injury to dormant plants.

The same winter, between December 3 and March 17, a series of nine experiments were carried out bearing upon the resistance of hibernant larvæ to submersion in water of ordinary temperatures. Pieces of heavily infested grape roots were placed in petri dishes under about 1 inch of water. The periods of submersion ranged from 48 hours (two days) to 1,512 hours (nine weeks). It was found that with the lengthening of the submersion period the percentage of aphids succumbing increased. A submersion of six weeks, however, resulted in the destruction of only 72 per cent of the aphids, one of five weeks in 64 per cent mortality, the final test (that of nine weeks) alone destroying all the aphids. In tests of from 48 to 168 hours' submergence the temperature of the water averaged 47° F., in the final test of nine weeks it averaged 55° F., and in four intermediate tests of from three to six weeks, 53° F.

In the light of the results of this series of tests the fact that a practical vineyard submersion requires at least two months' flooding is not a cause for wonder.

An observation made during the winter of 1913–14, from December to February, showed that hibernant larvæ can withstand short intermittent submersions in water interrupted by periods of low temperatures, even passing below 32° F.

On June 9, 1914, two experiments were conducted, bearing on the resistance of eggs of the radicicole to heated water. In four of these tests the length of submersion was 90 seconds, and the temperatures ranged from 112.1° to 131° F.; in the other seven, the eggs were submerged 60 seconds under temperatures varying from 108.5° to 132° F. Results showed that a temperature of 123° F., with an exposure of 60 seconds, destroyed all eggs. For practical use it is desirable to have a temperature of at least 125° F.

In the experiments the eggs after treatment were placed on pieces of vine roots and observed for possible development. Temperatures of 123° F. or over killed the eggs immediately, but the lesser temperatures killed none or only a variable percentage. Those eggs not killed hatched normally.

During June and July, 1914, a series of tests was made with radicicole eggs exposed to atmospheric temperatures varying from 76° to 90° F. for periods varying from 5 to 60 minutes. With a

shade temperature of 90° F., eggs exposed to sunlight were killed in 20 minutes. At a shade temperature of 76° F., 40 minutes' exposure to direct sunlight killed all aphids, but when placed in the shade the eggs resisted the maximum test of 60 minutes' exposure.

It is therefore apparent that eggs can resist the sun's rays to a considerable extent. The extent of their resistance to atmospheric temperatures in the shade can not be estimated, though it is of course greater than their resistance to direct sunlight. The eggs utilized in these tests were selected at random, and therefore were in various stages of embryonic development.

Experiments with the submersion in water of active newly hatched larvæ are detailed under the heading "Diffusion," which follows.

DIFFUSION OF PHYLLOXERA.

In European countries four natural means of diffusion are recognized: (1) By the winged insect; (2) by newly hatched wandering larvæ issuing from the soil; (3) by newly hatched wandering larvæ traveling through the soil; (4) by the gall-inhabiting form. To these there should be added casual means, as follows: Cultivating instruments, vine supports and picking boxes, plants between the vines, man and domestic animals, water, cuttings and rooted vines, phylloxerated land, and old stumps.

DIFFUSION BY FLIGHT.

Comparing the slower diffusion of the phylloxera in California with that of certain European vine-growing sections, it was from the first doubted that the winged form was a common diffusing agency, in spite of the fact that its production is often abundant in California vineyards on the roots of vines the second and third years after the initial infestation. This doubt became strengthened by (1) lack of leaf galls in nature and failure to discover winter eggs on a large number of vines of different varieties known to have been infested by migrants, or to have been close to vines thus infested; (2) the fact that, in confinement, during five years, thousands of migrants were utilized and only 72 sexual forms were secured, and, in turn, no normal winter eggs. On comparing the researches of European observers it is found, however, that in most cases they were unable to raise the sexual forms in confinement in any numbers, so this second point is inconclusive.

Grassi (11, p. 138–148) and his colleagues demonstrated that the insect which hatches from the winter egg always settles on the young vine leaf and becomes the gall-making stem mother (gallicole). They also found (11, p. 274–280) that there occurred a nymphlike form which deposited parthenogenetic eggs from which issued root-

feeding insects. This form generally occurred on resistant vines, but also on viniferæ along with the sexuparous migrants. The individuals exhibited much diversity in development, ranging from those with large wing pads to others bearing no vestige of wing pads, but having more fully developed eyes than the typical adult radicicoles. In nearly every case their eggs were parthenogenetic, the resultant larvæ becoming root feeders. This form has been styled "intermediate," in that it is intermediate in structure between the radicicole and the winged form. Observations indicate that it occurs rather infrequently in California. It has been discussed under the heading "Nymphicals or intermediate forms" (p. 82). All the fully winged individuals observed in California which deposited eggs were sexuparous.

To sum up, it is not believed that in California there is diffusion through the winged form. It is perhaps worth while to record some observations upon the behavior of the insects of this form in the vineyard. During July and August, 1914, these occurred in a Zinfandel vineyard badly infested with phylloxera. Previously roots of many of the vines on lighter soil had been dug up, and it had been found that a large production of migrants was developing, especially on vines having the external appearance of not being badly phylloxerated. The condition of the roots on this type indicated that phylloxeration had not been in progress more than two years and the tuberosities had not reached a stage of advanced decay; but phylloxeræ were abundant, and it was evident that another year would find the vines much less thrifty. Sticky paper, tacked to boards, was placed in the vineyards, both on the surface of the ground in a horizontal position and in a vertical position. The horizontal papers were placed beside infested vines at distances varying from 6 inches to 5 feet from the trunks. The vertical boards were placed throughout the infested part and outside of the vineyard and extended from the soil surface to a height of 7½ feet. More winged migrants were obtained on horizontal boards than on the vertical boards in proportion to a given area of paper. The majority of migrants caught on the horizontal boards were found at the edges, indicating that they reached the papers by walking rather than by flight. In some cases where individuals were found in the middle of the sticky papers it appeared that these might have fallen down from canes of the vine above, but in many instances the phylloxeræ obviously had reached the papers by flight or had been blown thither by the wind. Those on the vertical papers had either been borne by the wind or had flown voluntarily. On the vertical boards facing away from the prevailing wind no migrants were caught. Vertical boards with sticky paper were placed in the vineyard on the following dates: June 20; July 7, 10, 13, 21, 24, 31;

August 3, 7, 11, 14, 17, 20, 21, 31. Horizontal boards were placed July 10, 13, 21, 24, 31; August 7, 11, 14, 17, 21, 25, 31; September 5, 11, 26.

On the vertical boards eight migrants were captured between July 13 and August 21, and on the horizontal boards, between July 10 and August 17, 51 were taken. The area of paper exposed on the vertical boards was 63,725 square inches, almost 50 square yards, while that of the horizontal boards was 7,625 square inches, not quite 6 square yards. The papers kept sticky for about four days on the average. Considering the comparatively large number of migrants captured on the limited areas of sticky paper, there must have been a heavy infestation throughout the vineyard. Winged phylloxeræ were observed on and about the bases of vine trunks, and many were caught in spider webs and died. Whether the migrants deposit the sexual eggs in the vineyard or not, the total absence of galls on the vines (viniferæ and resistants) surely indicates that such eggs come to nought.

From rather meager observations it appears that the sexuals require a high temperature, coupled with considerable humidity, for their successful development, and that the climatic conditions of California lack the requisite combination.

DIFFUSION BY NEWLY HATCHED RADICICOLES ISSUING FROM THE SOIL.

In the summer of 1868, Faucon, in France, observed young radicicoles wandering over the surface of the soil following a heavy rain, which had caused the soil to crack open in drying. He also observed the phylloxeræ to enter cracks and disappear. In 1872, he again observed these phenomena between August 4 and September 30. The year following, his observations were made from June 14 to September 13, so that he was able to see wandering larvæ during a period of three months. In 1876, Boiteau, in France, confirmed the observations of Faucon, adding that he found that the greatest number of wanderers issued from vines at the periphery of the phylloxera "spot." Since then other observers have discussed the phenomenon of "wanderer" diffusion. Grassi (11, p. 351, 138, 148) and his colleagues, working from 1907 to 1911, conducted a series of experiments with the wandering larvæ. They found that these were strongly attracted to light and that in walking over the soil surface they did not go in a straight line, but deviated according to the variations of the surface. On a piece of glass they proceeded in a straight line and covered a distance of about 2 cm. the first minute.

As regards inoculation of vines by these wandering young, successful experiments were carried out in Europe on vines in pots, it being found that the wanderers penetrated the cracks formed between the inside periphery of the pot and the drying soil and infested

the rootlets growing in contact with the pot. Experiments showed that when sand was dry it obstructed the wanderings of the phylloxeræ, but when moistened the phylloxeræ might be drawn through it with the water. It was also found that in sandy soils water might occupy all the interstices between the grains of sand, repelling the phylloxeræ, whereas in soils of other types air cavities existed sufficient to enable the phylloxeræ to live.

In California the wandering larvæ were first observed in glass jars in which were kept phylloxerated roots in the summer of 1913. When such jars were removed from the darkness of the cellar to a light room, young larvæ were observed wandering up the sides of the jars. In the dark cellar such wandering took place, but after light was admitted to the jar the wandering became much accentuated. Similar wandering of larvæ was observed in the cages used for observations on living roots (Pls. V, VI, fig. 1; VII).

Until 1914 no vineyard observations in this direction had been made, but in that year wanderers were observed in their normal state. For these observations, vines in a phylloxera "spot" in a Zinfandel vineyard 10 years old were selected. This "spot" was situated on light clay loam upon sloping ground, and within its confines wandering larvæ were observed during July and August. These were found in greatest numbers coming from vines near the outer edge or periphery of the "spot." Such vines had little external evidence of phylloxeration, but upon examination it developed that the roots were heavily infested and produced many migrants as well as wanderers. From vines obviously moribund a smaller number of wanderers appeared. Wanderers also were obtained on the same horizontal boards with sticky papers on which migrants were caught. These were captured close to the edge of the sticky substance and never farther from it than 6 mm., and it appeared that all those taken had crawled to the papers and that none had been borne on the wind. On vertical papers, not even when placed within 2 feet of the wanderers, and to the leeward of them, were any phylloxeræ captured. It was observed, however, that on favorable occasions wanderers are easily borne off by gusts of wind. The part of the vineyard in which wanderer activity occurred was moderately well cracked through drying. On the horizontal sticky papers wanderers were caught at points from a few inches from the vine trunk to 5 feet from the nearest vine and directly in the center of a square described with a vine at each angle. In this latter case either the phylloxeræ had ascended by the trunk of the vines, and then walked 5 feet, or else they had ascended by means of cracks nearer the paper. In either case it is obvious that the spread of a given phylloxera "spot" may result from the activities of these wanderers without the agency of wind.

Wanderers were first caught on sticky papers July 21 and first observed alive in the vineyard August 11. After August 18, no more were caught on the sticky papers, and after August 25, no more were observed alive. The weather during July and August was for the most part bright and warm. In the vineyard the wanderers were observed in by far the greatest abundance near the trunks of the vines, and it appeared that they had reached the soil surface by following up the roots. No wanderers were observed on the aerial portions of the vines themselves. They showed much activity, wandering aimlessly around over the soil. They seemed to prefer the shaded parts, but appeared also on ground surface exposed to the sun. Large numbers were found dead close to the vine trunks, and these occurred in places where the soil was very fine, indicating that the phylloxeræ were unable to progress in fine soil. Laboratory experiments bore out this supposition. Many others became caught in spider webs stretched over the soil surface. The character of the soil in the vineyard in August, 1914, was such as to enable phylloxeræ to pass from one vine to another without necessarily encountering very fine soil, as no cultivation had been practiced since May, 1914, and the vineyard had been cultivated previously only in one direction.

As regards the capture of wandering larvæ upon sticky papers, the data given in Table XXXIV are of interest:

TABLE XXXIV.—*Wandering larvæ of the grape phylloxera; diffusion in vineyard; Walnut Creek, Calif., 1914.*

Date caught on paper.	Number of wandering larvæ caught.	Distance from nearest vine trunk.	Area of sticky paper on which phylloxeræ were caught.
		Feet.	*Square inches.*
July 21–24	3	5	135
July 24–28	1	2	135
July 31–Aug. 3	20	2	135
Do	1	5	135
Aug. 7–11	2	2	135
Aug. 11–15	1	½	135
Aug. 14–18	1	2	135

During the period from July 21 to August 18 many sheets of sticky paper 135 square inches in area (9 by 15) were placed on the surface of the ground, and wanderers were caught on 7 (see above) out of 32 papers. In the majority of instances the individuals were caught on the side of the paper toward the nearest vines, which would indicate that they arrived there straight from the trunk of the vine. On sides of the paper facing vines farther away it would be natural to expect fewer wanderers when one considers how the circumference of a circle increases in proportion to its radius, and also the comparatively equal diffusion of wanderers in all radii, if the vine

trunk is considered as the central point. On two occasions wanderers were caught on paper placed equidistant (5 feet) from four trunks of infested vines. Examinations showed that between one vine and another, even of apparently equal phylloxeration, a great variation in the production of wanderers took place. It also appeared that there was a tendency to produce these forms all at one time as though they had collected in a mass and then issued all together. As regards the time of day at which they were most abundant, it appeared that more might be observed between 10 a. m.[11] and 1 p. m. than at other daylight hours. European observers found that in general the wandering larvæ appeared in greatest abundance in the early afternoon, which is the hottest part of the day.

Vineyard observations were continued in 1915. The same vineyard was used, but more attention was paid to phylloxerated vines on the parts in which the soil was a heavy black clay. On this heavy soil no wanderers appeared before July 24, and none was found after July 29. The larvæ also were always very scarce, notwithstanding the fact that the soil contained numerous cracks which would enable the wanderers to reach the surface. On the lighter soil (clay loam), wandering larvæ first appeared July 14, and they continued to issue until August 18. During this period of over a month about two-thirds of the phylloxerated vines examined were producing wanderers. Between July 15 and 21 they were most abundant, as many as 20 or 30 living individuals being visible at one time beside the more heavily infested vines. In August hundreds of dead larvæ could be seen on the surface of the soil around the bases of the vine trunks, and large numbers were caught in spider webs. As in the previous year, the vines bearing the largest numbers of wanderers were those of recent phylloxeration.

In 1915, during the period of wanderer activities, the weather was for the most part quite hot and dry. Occasionally there were cool days, and on these the wanderers appeared to be as active as on the hot days.

It appeared certain that the great majority of the wandering larvæ ascended to the light by way of the main trunk of the vines, around which there occurred almost always a wide crack. More issued from Zinfandel vines than from Carignan vines equally phylloxerated, perhaps because the Zinfandel had thrown out more fleshy rootlets in May and June, and these had decayed in July while heavily infested. It would thus appear that many of the wandering larvæ are produced on these surface fleshy rootlets and leave them because they have become overcrowded or have started to decay.

In each of the years 1914 and 1915 wandering larvæ appeared in the vineyard over the same period, i. e., from the middle of July to

[11] All references to clock time refer to "Standard time."

the end of the third week in August. The condition of the soil was about the same in both years, moisture being somewhat higher than usual because of extra heavy precipitation each spring. The retention of moisture near the soil surface tends to produce many fleshy rootlets, and these in turn produce abundant nymphs and wandering larvæ. Thus a wet spring results in the early production of migrants and wandering larvæ.

A number of laboratory observations were made on the wandering larvæ. From these it appeared that the insects were capable of walking as much as 14 feet on a smooth surface, provided a strong light attraction was present. On fine soil their appendages became clogged very soon, and prevented further locomotion, but on hard surfaces, they progressed successfully. On warm surfaces they easily became "baked" to death, and in fact always lived the longest when least exposed to the sun, as the heating of the surface soil killed the aphids. Larvæ easily passed over wet sand and were able to make headway on dry sand, but could not penetrate sand. It was found that the larvæ could remain alive at least for three days, wandering around partly upon the soil and partly in cracks in the soil in a flowerpot subjected to an average amount of direct sunlight.

During the summer and autumn of 1914 a number of young rooted vines were planted in 9-inch pots, and these were inoculated during May and June by burying phylloxerated roots around the stalk or by transferring eggs to the larger roots. These vines included viniferæ, American nonresistants, and resistants. On the top of these pots and resting on the earth were fitted tightly circular pieces of wood with a hole in the center, through which passed the stalk of the vine. The whole aerial portion of the vine was inclosed in a muslin cage. This construction was designed to compel phylloxeræ ascending to the soil surface to make their way through the hole around the stalk; and having done so, they would be unable to escape by reason of the white muslin cage and would soon die. In October and November these cages were examined, and in some of them small numbers of dead wanderers were found, in others none, and in still others very large numbers. Those containing dead wanderers in abundance were the ones in which the vines had been fertilized with chemical fertilizers, and there was also a corresponding abundance of winged migrants from such vines. The action of the fertilizers produced many migrants and many wanderers and invigorated the vines, yet in all cases a large root infestation by wingless forms persisted through the winter following. In the cages above mentioned fertilizers, in liquid form, were applied periodically during the summer. In 1915 a similar series of vines were fertilized with solid fertilizers at the time of planting in early spring, and

later observations showed that wanderers were no more abundant on fertilized than on check, unfertilized vines. On young vines in pots wanderers were often observed to ascend the vine stalks to 6 inches above the soil surface, and in one instance on an American nonresistant vine (Golden Champion) several of them fastened on the bark and matured there (1914). This vine was never exposed to the brightest light and, moreover, during 1914, within a radius of 4 inches from its stalk was placed a glass cylinder, around the bottom of which was fastened 2 inches of black paper, so that the stem of the vine received little light. In 1915 the glass cylinder and black paper were removed and no wanderers settled on the aerial portion, although from June 29 to September 10 a limited number of them could be seen almost daily ascending the stalk to about 6 inches as in the previous year.

During 1913 and 1914 many instances were observed of wanderers infesting the rootlets in the pots used in the cages for observations on living vines (Pls. V–VII). In these cases the wanderers were produced on the exposed portions of the roots, and wandering off these, they found themselves on the surface of the soil in the pots. They then proceeded to pass down through the cracks around the inside periphery of the pot, where the soil had dried, and finally reached the rootlets growing against the inside of the pot. Such infestations occurred on rootlets from the surface to the total depth of 9 inches. This infestation occurred during July, August, and September, and in November, when the vines were pulled up, most of the nodosities produced by the phylloxeræ had rotted. In some cases rootlets appeared above the soil around the periphery of the pot, and these were infested easily and abundantly through the agency of wandering larvæ. In the pots in which quartz had been substituted for earth for experiments with fertilizers, the wanderers were able to find their way down to the rootlets, although the cracks in the quartz were fewer and narrower than in the earth. It may be mentioned that the earth used in the pots in 1913 was a rather heavy dark loam, mixed with sandy loam, and in 1914 only the heavy dark loam was used. A layer of gravel and sand about one-fourth inch thick was laid on the surface, but this did not prevent cracking around the inside periphery of the pot. The heavier soil of 1914 seemed to allow of easier passage for the wanderers.

In the spring and summer of 1914 three vine section cages containing cuttings were placed together in a trench. Two of these were infested with phylloxeræ throughout May and June. On July 18 it was found that a vine in the third cage was infested with two egg-laying adults, each situated on a nodosity. The vines in this section cage never had been inoculated, and it is certain that their in-

festation was caused by two wanderers from an adjoining cage. It was judged that this infestation must have occurred about June 20, when many eggs were hatching in the adjoining cages and many rootlets decaying, thus compelling the newly hatched larvæ to seek food elsewhere.

INOCULATIONS WITH WANDERERS.

On July 31, 1913, 30 wandering larvæ were taken from jars in the cellar and placed on pieces of sound severed roots in a petri dish. On August 13, 25 half-grown phylloxeræ found roaming around in jars were added. All the latter deserted the roots and died, but of the former, three matured August 25 to September 18. A later inoculation (Sept. 25) with 40 young wanderers resulted in none of these remaining. Another similar experiment was tried on September 29, with 40 young wanderers, but it also failed. Thus out of 135 individual wanderers only three matured.

In 1914 this experiment was repeated, and two pieces of sound severed roots were inoculated in a petri dish, one with 8, the other with 40 wanderers. In this case a layer of moist sand was placed below the roots, whereas in 1913, only filter paper had been used. Of the smaller lot 1 and of the larger lot 20 matured. Thus On August 28, 15 wanderers from jars in the cellar were placed on the living root of a Tokay, and 3 of these hibernated and developed the following spring.

In the autumn of 1913 an attempt was made to inoculate the roots of sound potted vines by means of wandering larvæ placed upon the surface of the soil in the pots. For this purpose, 35 wanderers were placed on the soil of each of four potted vines (Resistant hybrid, Sept. 18; Agawam, Sept. 23; Burger, Sept. 26; Thompson's Seedless, Oct. 6). In no case did the wanderers succeed in inoculating the roots. The soil, however, contained extremely few cracks.

The following year this phase was pursued further. Sound pieces of roots were planted 4 inches below the surface in four 9-inch pots. On July 8, 30 wanderers were placed on the soil surface of the first pot, the soil being cracked from having been watered the previous day. The root below was never infested. The soil of the second pot was watered to cause it to crack extensively. After it became well cracked about 25 wanderers were shaken on it, July 8. An examination of the root, August 25, showed it to be infested with a thriving colony of phylloxeræ. In the third pot the soil was not watered; consequently there was no cracking. On July 12, 50 wanderers were shaken out on the surface. No infestation of the root

below occurred. The soil of the fourth pot was watered sparingly, and few cracks were formed. July 17, 12 wanderers were shaken onto the soil. No infestation of the root below occurred. Only one out of the four experiments resulted positively, and in that one the soil was very well cracked, affording access to the root.

Inoculation of the wanderers on living vines was attempted through the following experiments: Five lots of four vinifera vines each were planted, two on light sandy loam and three on heavy clay loam. The vines were all young rooted vines, and they were planted roughly in the form of squares during the month of June. In the center in each one of four of the groups a phylloxerated vine (potted) was put in the ground at varying distances from the four surrounding vines. In one group the four outside vines were distanced, respectively, 14 inches, 2 feet, 3 feet, 3½ feet from the central vine. In a second group they were distanced, respectively, 2, 3, 4, and 6 feet from the central vine. In the third group they were distanced, respectively, 2, 4, 6, and 8 feet from the central vine. In the fourth group they were distanced, respectively, 2, 3, 4, and 6 feet from the central vine. In the fifth group the four vines were potted, and in place of an infested central vine, infested roots were buried 1, 2, 3, and 4 feet, respectively, from the outside vines. In this last case the vines were potted to prevent possibility of underground inoculation. The four central vines remained infested throughout the summer, but it was not disclosed that they, or the buried roots, produced any wandering larvæ above the surface. The surface of the soil in the area used for these experiments was kept well cracked. In no instance did the 20 outside vines become infested.

In 1915, field experiments were conducted in a vineyard which had several large phylloxera "spots" both on light and heavy soils. The light soil might be described as a silt loam with a clay admixture, and the heavy soil was black, sticky clay. In spring a number of sound rooted vinifera vines 1 year old were procured and planted in 5-gallon kerosene cans from which one side had been cut. Different types of soil were used in these cans. The vines thus planted were kept apart until July, when they were carried out to the vineyard selected and planted level with the soil at varying distances from vineyard vines from which wandering larvæ were known to be issuing. To insure cracking of the soil, water was applied to the soil surface and also to the soil between the cans and the near-by vine. Wandering larvæ were observed in this vineyard from the middle of July to August 20. In September, after the wandering of the larvæ had ceased, the cans were dug up. Table XXXV gives the results of this experiment.

TABLE XXXV.—*Field experiments on inoculation of vines by wandering larvæ of the grape phylloxera, Walnut Creek, Calif., 1915.*

No. of vine.	Type of soil in can.	Variety of vine.	Date of planting can in vineyard.	Date of taking up can in vineyard.	Distance of vine in can from trunk of infested vine in vineyard.	Result.
					Feet.	
[1] 1	Silt loam	Mission	July 14	Sept. 8	2	
[1] 2	do		do	Sept. 9	2	
3	do		do	Sept. 17	1	Uninfested.
4	do	Zinfandel	July 15	Sept. 8	1½	
5	do		do	do	5	
6	do		July 17	Sept. 9	2	Infested.
7	do		do	Sept. 15	1½	
8	Heavy black loam, 2 parts; silt, 1 part	Carignan	do	Sept. 9	1	Uninfested.
[1] 9	do	Zinfandel	July 20	Sept. 15	4	
10	do		do	do	1½	
11	Heavy black clay loam		July 21	Sept. 9	1½	
12	do		do	Sept. 17	1½	Infested.
13	do		do	Sept. 15	5	
[1] 14	Sandy silt		July 22	do	4	
15	do		do	Sept. 17	2½	
[1] 16	do		do	Sept. 15	2½	
17	Pure sand		do	do	2½	
18	Heavy black clay loam		July 24	do	1	
19	Sandy silt		do	do	1	
20	Heavy black loam, 2 parts; silt, 1 part	Carignan	do	do	1½	
21	Heavy black loam, 1 part; silt, 1 part	Zinfandel	do	Sept. 8	8	
22	Heavy black clay loam		do	do	4	
23	Sandy silt		do	Sept. 15	1	
24	Heavy black loam, 2 parts; silt, 1 part	Carignan	do	do	3	Uninfested.
25	do		July 27	Sept. 17	¾	
26	Heavy black loam, 1 part; silt, 1 part	Zinfandel	do	do	4	
27	do		do	do	2	
[1] 28	Pure sand		do	do	1½	
29	Sandy loam		do	do	1½	
30	do		do	do	5	
31	Heavy black loam, 1 part; silt, 1 part		July 29	do	2	
32	Heavy black clay loam		do	do	2	
33	Sandy silt		do	do	2	

[1] Entire vines died shortly after having been planted in vineyard, therefore can not be included in results of experiment.

Of the 27 vines which were alive when the cans were taken up, 21 had been planted in the phylloxera "spot" on light soil and 6 in phylloxera "spots" on heavy black clay. None of the latter and only 4 of the former group became infested. Vine 6 was examined September 9, and an infestation consisting of 1 adult radicicole and about 12 larvæ was found. This indicated that a single wanderer had established itself on the vine. On vine 11, on the same date, there were found 3 adults and about 20 larvæ. On vine 12 on September 17 there were 6 adults and about 200 larvæ, besides many eggs. On vine 13 on September 15 there were over 350 phylloxeræ, including some 50 adults. Vines 11, 12, and 13 were planted around the same infested vine. In the case of vine 13 the infestation was started either by a large number of wandering larvæ in August or more likely by one or two wanderers directly after the vine was planted on July 21. Since in August the phylloxera generation cycle may be passed in less than 22 days, and since each mature radicicole may average 8 eggs per diem for several weeks, it would have been possible for the infestation on vine 13 to have developed

from a single wanderer. Similarly, it is possible that the infestations on vines 11 and 12 originated with one individual each.

In all of four inoculated vines the infestations were confined to the larger roots, and there was no nodositous infestation such as occurred with wanderer inoculations in potted vines at the laboratory. This is explained by the fact that the soil in the cans did not crack deeply enough to reach the rootlets (none of which came near the soil surface) while it cracked badly around the base of the stems of the vines. It is therefore most probable that the wandering larvæ passed down the vine stem. Cracks of 1 foot or more in depth were quite abundant in the vineyards in July and August, and it was possible to find rootlets such as form nodosities when punctured by phylloxeræ at a depth of 6 inches from the soil surface. At that time of year there is generally in the vineyards a wide crack about the base of the vines, and it is through these cracks that the great majority of the wandering larvæ ascend to the surface. In the vineyard a wanderer could never be kept under observation long enough to be sure that it entered a crack permanently, therefore, with the purpose of seeking a root. Wanderers readily enter any crack which they can not bridge but frequently reappear after a short period of time. In pots they have been observed to enter whatever cracks they encountered, subsequently inoculating roots buried below. In other experiments with pots the wandering larvæ have been found to crawl down the crack between the soil and the inner side of the pot and inoculate the rootlets growing around the inside of the pots. Also it has been observed that in the vineyard experiments the inoculation was probably made by the wanderers crawling down the stem, since no other available cracks were favorable. In the vineyard, therefore, it is assumed that the wanderers enter the first crack they encounter.

In the experiments of 1914 with sticky papers, wandering larvæ were captured at varying distances up to 5 feet from the nearest infested vine. The four inoculated vines the year following were 2, 1½, 1½, and 5 feet, respectively, from the nearest infested vines. It should be said that there was a possibility that the infestations were inoculated by wanderers coming from infested vines at a greater distance. In the instance of the three inoculated vines planted in cans around one single vineyard vine it is reasonably certain that all three became inoculated from the central vine. From this vine large numbers of wanderers were observed to issue.

No vines were planted more than 5½ feet away from a vineyard vine, the vineyard being planted 8 by 8 feet.

The soils used in the cans were of different types, but no satisfactory conclusions were drawn from this feature. It was noted that the

vines planted in lighter soils grew poorly and that the percentage that died was greater than in the case of heavy soils.

In 1914, wanderers were taken from jars in the laboratory cellar and successfully colonized on pieces of roots. It was found that they developed into the usual type of radicicole phylloxeræ. In order to ascertain definitely the future of wanderers observed in the vineyard a thrifty section of sound grape root was transported to the vineyard on July 17, 1915, and 12 larvæ, wandering upon the surface of the soil, were placed thereon. Four of these subsequently matured as wingless radicicoles between August 23 and 27, and before the advent of winter a considerable colony was established. A contemporary experiment of similar nature was carried out with a like result with larvæ taken wandering on the surface of the soil in pots containing infested vines.

In conjunction with the inoculation experiment in the vineyard four Zinfandel vines were planted in kerosene cans in the laboratory yard, and after watering to insure soil cracking they were inoculated artificially by placing the larvæ on the soil surface. These inoculations comprised, respectively, 21, 190, 300, and 625 wanderers collected during the summer. Two of the cans contained sandy silt and two heavy black clay. In no case did infestation result.

For another experiment two galvanized-iron cans, 4 by 4 inches, and 10 inches deep, were used. Sound pieces of vine root were placed in each, 7 inches below the soil surface, and the cans then filled to the top, one with sandy silt and the other with heavy black loam, after which the cans were buried, their tops at a level with the soil surface. The surfaces were watered to insure cracking of the soil. Between July 15 and August 4, several hundred wanderers were placed on the sandy silt, and between July 18 and August 4 several hundred on the black loam. On August 27 the roots in the cans were examined. Those buried in the sandy silt which had failed to crack much were uninfested, while those buried in the heavier soil bore a small infestation, indicating that one or more wanderers had penetrated to the roots.

From the results of experiments on natural and artificial inoculations of vine roots by wandering larvæ through the soil two facts stand out: (1) Notwithstanding the large numbers of wanderers available or utilized, positive results were infrequent. In the years 1913, 1914, and 1915, altogether 14 vessels containing vine roots, either living or cut into sections, were inoculated by placing wanderers on the soil surface, and only two of these gave positive results. The average number of wanderers used for each vessel was about 150. In the vineyard experiment in 1915, only 4 of 27 exposed vines became inoculated, yet all these vines were planted near vineyard vines

from which wanderers were issuing. It is true that the soil surface inside the cans was a small area—126 square inches—and that the soil itself was not as thoroughly cracked as it might have been; but in many instances the cans were not more than 1 foot from the trunks of the infested vines, therefore, from the wanderers when they issued, whereas in vineyards vines are set 6 or more feet apart. (2) The presence of cracks in the soil leading directly to roots is necessary to permit the wandering larvæ to descend to roots, for the larvæ can not dig their way through the soil, and during the period when they are issuing, rain, which might provide moisture to draw them into the soil or wash them onto exposed roots, is lacking.

The writers are of the opinion that wandering larvæ are the cause of considerable local spread of phylloxera, that is, within the vineyard or district; and that they are instrumental in causing the formation of new phylloxera "spots" or foci. Under favorable conditions it has been proved that they may live for at least three days above the surface of the soil, and thus may be transported from place to place with the possibility of finally becoming located on a vine root. There is no reason why wanderers may not live for as long as two weeks on the soil surface without feeding, provided this surface is not heated by the sun. In one instance, after being placed on a piece of root, several of them wandered for as many as five days before settling down to feed. It may be said also that larvæ have been found to live in water as long as nine days without food, and it may thus be assumed that they might remain as long in the open air under average conditions of temperature and humidity. This fact would explain how the insect may be spread from one locality to another by wandering larvæ that lodge in such vine material as picking boxes (see following under "Casual agencies of diffusion," p. 115).

There are certain marked instances in California vineyard districts where phylloxeration has developed "with the prevailing winds." The only wind-borne forms of the phylloxera in California are the winged migrants and the wandering larvæ. The California biology indicates that the migrant has no bearing on the preservation of the species, and therefore such phylloxeration has resulted from wind-borne wandering larvæ.

DIFFUSION BY NEWLY HATCHED RADICICOLES TRAVELING THROUGH THE SOIL.

In 1914, experiments on subterranean diffusion were conducted. In April three Muscat rooted vines were planted in a 4-foot square box containing heavy loam covered with a 3-inch layer of fine sand. The sand was used for the purpose of preventing wandering larvæ from emerging upon the surface and reaching the sound vines. May 20,

one of the vines was artificially inoculated. The second vine was 1 foot distant, and the third 2 feet distant from the first. On October 10, all three vines were dug up, and it was found that the first had a small infestation all over the root system. The second vine had a small infestation chiefly on nodosities on roots nearest those of the first vine. So far as could be observed, the roots of the two vines did not approach nearer than 2 inches at the closest point, but as some of the terminal rootlets had died during the summer and autumn it is quite possible that earlier in the season rootlets of the two vines were contiguous. The third vine was uninfested. Its roots had been separated from those of the first vine by at least 12 inches and from those of the second vine by at least 5 inches.

This experiment did not appear to show that subterranean infestation was a common mode of diffusion. The condition of the roots on the first vine when it was pulled up showed that its summer infestation had been large and that many wanderers had been produced; therefore, one would expect that some of these would have found their way to both of the other two vines. The earth at the time of planting, however, had been packed very solidly, and the layer of sand prevented cracking so that there were very few, if any, subterranean passages affording access to the phylloxeræ.

The following experiments also were made: On May 22 two young viniferæ (Feher Szagos) were planted in a galvanized tin, 8 by 8 by 10 inches. Two sides of this tin were basally produced in the shape of a cone (Pl. VI, fig. 2, p. 52), and at each apex was a hole of one-half inch diameter. The cones were then tightly fitted into wooden tubes, through the centers of which ran a square passageway of one-half inch diameter, and the junctions cemented. The cones and wooden tubes were buried 8 inches below the soil surface. At the farther ends of the two wooden tubes similar galvanized tins were connected, and in each of them was planted a single sound vine (Feher Szagos). In this experiment the tubes were, respectively, 2 and 10 feet in length. The conical projections were expected to draw the roots toward the hole, therefore toward the tubes. No earth, except for about 2 inches at the ends, was placed in the passage in the tubes. Black paper was glued on to the top of the outside of the wooden tubes so as to prevent entrance of light. Thus the phylloxeræ, if they passed through the hollow inside of the tube, would not be influenced by any light rays. On September 23 the tins and tube were pulled up and the vines examined. Both central vines inoculated in May were well infested. Their rootlets and those of the two end vines had penetrated not more than 3 inches into the hollow of the tube, but in all four cases rootlets were abundant inside the conical projections. The vine at the end of the 2-foot tube was well infested with

radicicoles in all stages and with a few nymphs, indicating that the original infestation occurred at least before August 1. The vine at the end of the 10-foot tube was uninfested and showed no indications of ever having been inoculated.

On May 22 a similar experiment, with single vines (Carignan), was started, the length of the wooden tubes being 6 and 14 feet, respectively. On September 30 the vines were examined and the roots of the central vines were found to be well infested. Rootlets of all four vines had penetrated not over 3 inches into the hollow interior of the tubes. The vine 6 feet distant from the infested vines showed a good infestation, whereas the vine 14 feet away was not infested.

Thus, wandering larvæ, in two cases out of four, had found their way along the whole length of the interior of the tubes and had inoculated the roots at the farther ends of such tubes. The inoculated vines were those at the ends of the two shorter tubes (2 and 6 feet), and the sound vines those at the ends of the two longer tubes (10 and 14 feet). Thus it would appear that there is a limit to the distance over which the phylloxeræ will proceed when they have left a root, intent on finding new food. These experiments with wooden tubes demonstrated the wandering habits of the young radicicoles, and it may be readily understood how this subterranean movement may cause a phylloxera "spot" to enlarge, especially when the soil is cracked to any depth.

DIFFUSION BY YOUNG GALLICOLES.

In districts where the gall-inhabiting forms (gallicoles) are found, they may be the cause of diffusion. Either the branches of vines intertwine and the young gallicoles pass thus from one vine to another, or the young gallicoles are carried by the wind on to foliage of other vines or to the ground. Since the gall-inhabiting form is normally absent in California, this means of diffusion will not be discussed further.

CASUAL AGENCIES OF DIFFUSION.

CULTIVATING INSTRUMENTS.

During May and June badly phylloxerated vines are accustomed to put forth an abundance of short fleshy or fibrous rootlets close to the surface of the soil. Usually these are infested heavily with the progeny of the overwintered phylloxeræ. The vineyards usually are cultivated and hoed at this time, and these surface rootlets are frequently broken off and carried along by the cultivator and hoe. This possible means for spreading the insect having been considered, a series of experiments was initiated as follows: On May 30, in the vineyard, pieces of infested fleshy surface rootlets were secured, placed in earth, and the whole transported to the laboratory. Four

lumps of earth and roots were partially buried in the soil of a pot containing a young sound vine (Pierce Isabella). The earth and roots exposed to the sun quickly dried up and no infestation to the vine resulted. It may be stated that the diameters of the lumps varied from one-half to 2 inches. On June 4 the experiment was repeated, but the infested fibrous rootlets were wrapped loosely in four lumps of earth with diameters 1½ to 2 inches, and half buried in the soil of a pot having a sound vine (Cornichon) growing in it. The rootlets kept in good condition and the phylloxeræ lived four days (one of which was cloudy and rainy). On September 3 it was found that the vine showed a rather scanty infestation. On July 16 many strongly infested fleshy rootlets found in the vineyard, from 4 to 8 inches below the soil surface, were inclosed in a large piece of earth, half buried in the soil of a pot in which grew a sound vine (Carignan). On September 3 the vine was found to be strongly infested, especially on its upper rootlets near the inner periphery of the pot. On July 17 the experiment of the day previous was repeated in its entirety, with a Pierce Isabella vine, and on September 3 this vine was found to be severely infested, bearing many nodosities both on the upper and lower rootlets. Thus in three out of four attempts success was obtained in securing an infestation upon sound vines by placing pieces of infested rootlets in lumps of soil half buried in the earth of the pots in which those vines were growing. In practice it would very frequently happen that such rootlets severed by a cultural instrument would be buried several inches deep after being dragged along by the instrument. It is easy to understand how the insect might be diffused in this manner.

VINE SUPPORTS AND PICKING BOXES.

Vine supports or stakes (universally used), by reason of the fact that they enter the soil contiguous to the main stem of the vine, are very likely to bear phylloxeræ upon them. Since the newly hatched larvæ can live for at least three days, and probably many more, out of the soil and when not exposed to the sun's rays, it is apparent that infested stakes could be transferred to a considerable distance and when set out in a vineyard upon their arrival could be the origin of phylloxera infestation.

Many growers have declared that in their vineyards the phylloxeræ first showed evidence of their presence at a point or points where picking boxes coming from infested vineyards had been piled. If picking boxes were scattered in an infested vineyard during the time of the aerial wanderer migration, one can readily see that the opportunity would be afforded for the phylloxeræ to climb upon them, later to be transported to other vineyards, since it is a common

practice to use the same boxes many times in the picking season, and the same boxes may be used in more than one vineyard or district. In California, wine grapes are rarely picked before the middle of September, and raisin grapes are picked toward the end of August. In the experimental wine-grape vineyard, wandering larvæ were not found issuing after August 25, but in young vines in pots they were collected well into September. The fact that the wanderers were not found issuing in the wine grape vineyard at the time when picking boxes were distributed to a certain extent invalidates the theory of spread by these boxes. It is within the realm of possibility, however, that the latest issuing wanderers remained active and alive until the boxes were distributed some two weeks later. Observations on wanderers issuing from potted vines lead to the conclusion that the natural period of wanderer issuance may be considerably lengthened beyond that which was found to obtain in the experimental vineyard during the years 1914 and 1915. This longer period would include the time of picking wine as well as raisin grapes.

PLANTS BETWEEN THE VINES.

Walnut trees planted in vineyards indicate the possibility of diffusion through the agency of plants. The long roots of the walnut offer facilities for phylloxeræ to spread whenever vine roots come in contact with them or are very close to them. That phylloxeræ have been found moving on these roots would indicate that the latter often provide an underground channel of diffusion.

MAN AND DOMESTIC ANIMALS.

The possibility of the portage of phylloxeræ by man and domestic animals should not be overlooked. The winged forms and aerial wanderers may be blown on clothes or animals, and thereby spread, or they may be picked up with wet earth. This latter chance is greatly lessened under California conditions, because during the months in which wanderers and winged migrants are produced, the surface soil is dry, and the winged migrant is not a factor in diffusion.

WATER.

Recognizing the possibility of the spread of phylloxeræ through the agency of flowing water, the writers conducted the following experiments in 1914: From May 5, 11 a. m., to May 6, 11 a. m., a piece of severed root, infested by six adult overwintered phylloxeræ and about 100 eggs and larvæ, was subjected to a stream of water for the most part playing directly upon the insects and flowing 6 feet to an uninfested vine (Catawba) so as to effect contact with some of its roots and

also to stand on the surface of the soil about its stem. Examination of the piece of severed root after the experiment was concluded showed that about 40 eggs and young had been washed off. Five of the adults suffered no injury from exposure nor did most of the remaining young and eggs. On July 12 the Catawba vine was found to bear a strong nodositous infestation. On June 6, for eight hours, two pieces of severed roots bearing a total of about 200 phylloxeræ were subjected to a similar stream of water which subsequently flowed 6 feet to a sound Mission vine. On the severed roots the majority of aphids were not washed off. In this instance the roots of the living vine were not bared, and there were no cracks on the surface of the soil around it. On July 27 this vine was examined and found to be uninfested. The third experiment took place July 29. For eight hours two pieces of severed roots bearing a total of about 250 phylloxeræ were subjected to a stream of water which subsequently flowed 10 feet to a sound Feher Szagos vine growing in a pot. The surface soil in this pot had been previously watered, and thus was cracked. After the experiment was concluded, it was found that very few of the phylloxeræ had been carried off the severed roots. September 16 the vine was examined, but it proved to be quite uninfested. In each of these three experiments a fine stream of water was used and the angle of declivity was slight. In the first experiment only, wherein the roots of the living vine were actually exposed to the stream of water, did an inoculation through water agency occur. It is evident, however, that diffusion may occur by means of water-borne phylloxeræ. In the California vineyards such a condition could arise normally only between November and May, for in the other months it is very rare to have rain in any abundance. In April and May, however, when the phylloxeræ are active, heavy rains occasionally occur, and sometimes on the hillside vineyards deep waterways are formed, exposing the roots of vines to a depth of more than a foot.

In this connection some laboratory experiments were made upon the resistance of eggs and larvæ to water exposure. For this purpose small-sized glass vials and distilled water at about 64° F. were used. In one instance, in a corked vial, 9 out of 12 eggs hatched from 2 to 10 days after they were placed in the water. All those that hatched remained on the surface, while those that failed to hatch went to the bottom of the vial. In another instance eight recently deposited eggs were placed on the surface of the water in an uncorked vial. Six days later all had sunk to the bottom, but subsequently hatched. In a third experiment 11 well-advanced eggs were placed on the surface of the water in an uncorked vial. After 11 days all the eggs had hatched, six having remained on the surface and five having sunk to the bottom. In all three experiments the hatched larvæ failed to fasten to pieces of roots provided for them.

In a fourth experiment 26 eggs were placed in water in a stender dish. Two days later all but four eggs had sunk, but subsequently all eggs hatched and none of the resultant larvæ settled on the roots provided for them.

Table XXXVI indicates the results of experiments bearing on the behavior of newly hatched larvæ in water.

TABLE XXXVI.—*Behavior in water of newly hatched larvæ of the grape phylloxera, Walnut Creek, Calif.*

Date placed in water.	Number of individuals that—		Length of submersion.	Number of individuals after submersion.		Remarks.
	Sank.	Remained on surface.		Alive.	Dead.	
			Days.			
May 12	5	3	1	8	0	In stender dish without cover.
12	4	2	2	6	0	In small vial—uncorked.
27	2	0	2	2	0	Do.
15	4	2	3	2	4	In small vial—uncorked; sunk aphids dead.
19	5	1	3	1	5	Do.
June 1	4	2	4	1	5	In small vial—uncorked; sunk aphids alive.
May 24	1	1	5	1	1	Do.
June 1	0	4	6	3	1	In small vial—uncorked.
16	5	1	7	5	1	In small vial—uncorked; sunk aphids alive, but none subsequently fastened on root.
16	5	2	7	0	7	In small vial—corked.
1	0	4	9	1	3	Do.
July 15	6	2	4	8	0	In small vial—corked; one aphid subsequently matured Aug. 12 on severed root.
15	6	2	4	8	0	In small vial—uncorked; one aphid subsequently matured Aug. 11 on severed root.

NOTE.—In all except the first experiment, distilled water was used; in the first experiment, tap water.

Prior to June 16 the phylloxeræ were not followed up after their submersion to see whether they would fasten to the pieces of roots provided for them because the experiments were made only to ascertain how many of the larvæ would be alive after submersion. It may be noted that in some cases the larvæ which sank were found to be alive when removed from the water and in others those that floated were living when removed. The phylloxeræ survived as many as nine days on the surface of the water, and as many as seven days when submerged, and at the bottom of the vial. The experiments, however, did not continue beyond nine days, and there is no reason to believe that the insects could not live in the water many days longer than that period. The fact that they did survive as long as a week was sufficient evidence of the importance of their resistance to water. The two experiments of July 15–19 demonstrated that after four days in water the young larvæ could settle on pieces of roots and later mature. In the seven-day experiment, none settled on the roots. In all except one of the vials distilled water at about 64° F. was used. The behavior of the young phylloxeræ in water was characteristic. Those on the surface were active,

swimming around in circles, but those at the bottom remained almost motionless unless disturbed.

To sum up, it appears: (1) That eggs of radicicoles hatch readily in water, floating and sunken; (2) that the newly hatched larvæ may live for more than a week submerged, or on the surface film; (3) that these larvæ are capable, at least after four days of exposure to water, of fixing upon roots and developing in a normal manner. Further proof of the ability of young phylloxeræ to live submerged occurred in an observation made from September to November, 1914. A Riparia cutting had been placed in a glass vial in the laboratory. Immediately a callus formed, and many rootlets grew around the inside of the vial. On September 15, 20 eggs of radicicoles were floated on the water surface. None of the resultant larvæ persisting, more eggs were floated October 10. October 12 the water had evaporated, and four days later two young larvæ had settled. These had hatched after the water evaporated. About 1 inch of water was then poured into the vial to cover completely all the rootlets and the two phylloxeræ. October 22, three larvæ were observed under water, one of which had been fixed since October 16. October 27, there were visible under water, besides the original larvæ of the 16th, six additional larvæ, five of which were settled. October 30 all seven observed on October 27 had settled and an eighth was visible moving over the rootlets. A small tuberosity had been set up by one of the phylloxeræ. All the unhatched eggs had died. It was noted that when the insects were exposed to sunlight they moved their appendages actively. November 2, three settled larvæ were visible. These included the individual on the tuberosity and the one which had settled October 16. All others were dead. November 10 the only survivors were the original settler and the individual on the tuberosity. Shortly after November 20 all disappeared. Thus one individual, destined apparently to hibernate, persisted more than a month fixed on a root under water, and several others lived under water from 3 to 14 days.

There also exists the possibility of infestation by seepage. On vineyards of porous soils young larvæ on the surface may be drawn into the soil in time of a storm or irrigation. Also on steep hillside vineyards in the springtime, when heavy rains may fall or when a rise and fall in the "water table" may occur, a seepage infestation may take place. Any artificial irrigation during the months June to October invites the spread of phylloxeræ because in this period phylloxeræ occur above the surface of the soil or are active on surface rootlets.

CUTTINGS AND ROOTED VINES.

In European countries where a small percentage of the winter eggs are deposited under the bark of yearling wood there is a slight

danger of phylloxera infestation following the planting of a cutting from such wood. This danger does not exist in California, provided the cuttings are not "heeled in" before transportation, because the winter egg does not persist successfully. If the cuttings are "heeled in" before transportation in an infested district, the possibility of their becoming phylloxerated exists. Similarly, the possible danger from gallicoles remaining upon the foliage of canes late into autumn is nullified, because the gall-inhabiting forms do not normally occur in California.

The greatest danger of phylloxeration resides in the planting out of infested rooted vines. This is a very abundant means of distributing phylloxera. Even if only one or two out of a thousand vines are infested at planting, a "spot" or "spots" will form within a few years, and the whole acreage eventually will become infested. While the vines remain small, diffusion is slow because the roots of one vine are separated from those of its neighbors, and underground diffusion thus is rare if not impossible. Also, the relatively small number of roots, coupled with the relatively small number of phylloxeræ able to flourish thereon, prevents many opportunities for aerial diffusion by wanderers. If the majority of the vines planted out contain phylloxeræ, however, the vineyard's complete phylloxeration is not long removed. In a phylloxerated district the employment of resistant roots obviates the necessity of treating the vines before planting out in the vineyard, yet danger exists in cases where grafted vines are planted too deeply and the stouter vinifera scion is enabled to send out its own roots, in many instances crowding out the roots of the resistant stock. The scion's roots, being nonresistant, decay when phylloxerated just as though no resistant stock had been employed, and the expense and trouble of the grafting process are wasted. Even though phylloxeræ live on resistant stock roots in grafted vineyards without necessarily injuring the crop or vines, there still remains the possibility that infestation will arise from these grafted vines and that nongrafted vineyards near by will become inoculated. Such a possibility is accentuated the greater the proximity of two such vine areas, and especially if the nonresistant area is to leeward of the grafted area or if water flows from the grafted to the nonresistant vineyard. It is advisable, therefore, to disinfect even resistant roots when these are to be planted in a region free from phylloxera.

PHYLLOXERATED LAND.

Experiments with potted vines have given proof that phylloxeræ may live at least 10 months on buried severed pieces of roots, and also that such pieces may remain sound for 18 months and at the termination afford acceptable food for the insect. It is evident, there-

fore, that the planting of vines on land from which phylloxerated vines have recently been pulled up is a dangerous procedure. It is next to impossible to pull up grapevines without leaving pieces of roots in the ground. In the case of vine nurseries, this danger is very apparent.

OLD STUMPS.

Since the phylloxeræ may live under the bark of vine stumps to several inches above the soil surface, it is apparent that these infested stumps might possibly be a means of diffusion if sound vines should be placed near them. Such stumps, however, soon decay after they have been pulled from the ground and severed from their roots. In the active season, however, any insects dwelling upon them would hasten to leave and seek other food, so that in this season it is quite possible for diffusion to occur from the stumps. In the winter the phylloxeræ would all be hibernants, and these would die as the stump decayed.

SUMMARY.

HISTORY.

The grape phylloxera was introduced into California about the year 1858, having been brought on vines imported by settlers from the East. It thus appears that the pest arrived on the Pacific coast at least as early as it reached France, where the first evidence of its activity was vaguely noted in 1862.

For many years previous to this introduction the Spanish settlers and Missions had cultivated on a moderate scale the Mission grape, and this, though a very susceptible variety, as was afterwards proved, had flourished without disease. About the time of the advent of the phylloxera grape culture was receiving a great impetus, and many European varieties were being introduced which shortly showed signs of disease in localities in which the eastern vines had been planted.

The phylloxera has since spread throughout most of the grape districts of California wherever conditions have been suited to it, but never has the pest assumed such disastrous proportions as it did during the first years of its ravages in France. It is possible that the insect has never reached such isolated vine districts as those of the southern California counties, but in many of such isolated localities the conditions are unsuited to the insect, and thus we can not be certain that it did not reach these places and fail to establish itself.

Coming upon the scene at the infancy of the commercial grape industry, the phylloxera has been present throughout the growth

of that industry and, it is estimated, has in the course of some 60 years destroyed about 75,000 acres of grapes.

In many instances the insect has been distributed through the agency of infested rooted vines imported into an uninfested district or vineyard. In other cases the insect has been carried on vineyard material. In no instance has the distribution been as rapid as that which took place in the vineyard districts of France. The modified life cycle in California, i. e., sterility of the winged form, coupled with topographic barriers, consisting of mountain chains and dividing valleys, is in very great part responsible for this.

VINEYARD DESTRUCTION.

There is great variation in the rapidity of the destruction of vines and vineyards by phylloxera.

Apart from some variation in the different grape varieties, soil conditions must be considered as of great importance. In poorly drained soils the vines succumb much more rapidly than in well-drained land. Accumulation of moisture in the subsoil materially assists in the decomposition of infested roots, whereas if the subsoil is well drained, vines may flourish notwithstanding infestations extending over many years. Vines attacked when young and before their root systems have become established will succumb more rapidly than will those infested at a greater age.

The first indication of phylloxera in a vineyard occurs in the form of one or more stunted vines and a premature yellowing of the foliage. In time, adjacent vines will show similar indications, and those first infested are more noticeably stunted. Gradually more and more of the surrounding vines are affected, and those in the center become very much weakened or die outright. Thus are formed the so-called "oil spots" or foci for the distribution of the disease, which may be likened to the ever-increasing concentric circles of waves that are formed when a stone is cast into placid water.

Following the initial infestation of a vine under favorable conditions for phylloxera, the insects multiply rapidly, and within two or three years increase their range to involve the entire root system. Those which settle on the growing rootlets form fleshy lesions or swellings, which are termed nodosities. These swellings are generally somewhat curved, the insect inhabiting a depression of the inner arc. In the great majority of instances the insect stops further apical growth of the rootlet, and thus the rootlet ceases to supply nourishment to the vine. Although the percentage of rootlets thus infested is often large, a vine of vigor can easily send out more and continue to draw its nourishment from the soil. Other phylloxeræ settle on the older roots and in most cases cause swellings termed tuberosities,

which vary in size, but the majority are about one-fifth of an inch in diameter. They are frequently very abundant, and two or more may coalesce. The bark of the root often cracks longitudinally, and a chain of swellings arises from phylloxera punctures. As long as these swellings remain fresh, the health of the vine is not much impaired, but as soon as they decay the vine is injured, and when they decay in numbers the roots are frequently destroyed, causing first the stunting and subsequently the death of the vine.

BIOLOGY.

The grape phylloxera was named in 1855 by Fitch in America from the gall-inhabiting form, and in 1868 by Planchon in Europe from the root-inhabiting type. In 1870 Riley and Lichtenstein proved that the two forms were two separate phases of a single species; consequently, Fitch's specific name *vitifoliae* must be conceded priority.

In its native region, eastern North America, the insect has a very complicated life cycle, which includes an aerial gall-inhabiting form. In California the gall form has been observed only once and that in the year 1884.

The California life cycle (fig. 10), as indicated by research, is much more simple than that which obtains in the East, and as far as the economy of the insect is concerned, is purely parthenogenetic.

Winter is passed in the form of the hibernant larva. Virtually all hibernants are newly hatched larvæ which settle down to hibernate immediately after hatching from the egg in the autumn, but a few hibernate in an older stage. Coincident with the first flow of sap in spring, these hibernants commence to feed, and mature on the average five and a half weeks later. The hibernant larva is light brown in color, and is about one-third millimeter long and half as wide. The mature hibernant is about 0.75 mm. long and 0.40 mm. wide, and does not differ from the adult radicicole of any other generation. On the average, it takes the hibernant six months to mature, the period ranging from four and a half to seven and a half months. The mature hibernant gives rise to a number of generations—as many as eight—of root-feeding phylloxeræ throughout the summer and autumn. Although somewhat arbitrary, April 15 to October 15 best indicates the period of the active half-year of the insect, the period October 15 to April 15 being the dormant or hibernating season.

All forms of the phylloxera are oviparous. The average number of eggs per adult radicicole is about 110 and the average egg-laying period about 45 days. Incubation varies with temperature and lasts from 5 days in midsummer to over 30 days in December. The eggs

are lemon yellow and oval. Upon hatching from the egg, the bright-yellow larva seeks food. Larvæ hatching in spring mostly settle near the eggshells, but in summer and autumn a considerable percentage travel along the roots or forsake the vine altogether, either following cracks in the soil to reach neighboring vines or ascending to the surface of the soil and traversing the ground in their endeavors to reach other vines. To those that voluntarily forsake the vine has been given the term " wanderers." The larvæ molt four times, and on the

FIG. 10.—Diagram to illustrate annual life history: Innermost shaded crescent, active period of wandering radicicole larvæ; middle shaded crescent, period of development of the sexuparous migrant; shaded portion of outer circle, hibernation period of radicicole larvæ; unshaded portion of outer circle, period of active life on the roots.

completion of the final molt become mature insects. At first oval, they tend to become pyriform as they grow. The color, yellow, yellowish-green, or yellowish-brown, is dependent on the nature of the food. The length of the developmental period varies according to food and meteorological conditions. On succulent living roots the average period of larval development was found to be about 22 days (hibernant generation excluded), and the maximum and minimum respectively 36 and 10 days.

The winged form is produced from the middle of June until November. It is more abundant in the coastal districts than in the interior valleys. In their first two instars the larvæ of the winged form do not differ from the corresponding stages of the wingless form, but in the third and fourth stages they differ structurally, and in these stages are termed, respectively, prenymph and nymph. Both these forms are elongate in shape and are light greenish-yellow or yellowish-brown. The nymphs have two pairs of grayish-black wing pads. The winged insect is orange in color with grayish-black head and thorax and two pairs of scantily veined wings.

The nymphs transform in most instances near the surface of the soil and the winged migrants issue on the surface and fly about in the vineyard and neighboring regions.

The winged insects deposit eggs of two kinds, viz, male and female, and the insects which mature from these eggs are the true sexes. These forms are unable to take food, and under normal conditions mate upon reaching maturity and the female forthwith deposits a single egg under the bark of the vine. This egg hatches in spring and gives rise to a series of generations of gall-inhabiting and gall-making wingless aphids. A certain percentage of larvæ born in the galls, however, migrate to the roots before taking food, and in this way the species returns to the soil.

In California, under natural conditions, it is doubtful whether any sexes mature and still more doubtful whether any winter eggs hatch. Laboratory experiments indicate that the sexes mature in about 12 days.

In the late autumn, along with the nymphs are found curious forms intermediate in appearance between adult radicicoles and nymphs. These are called intermediates or nymphicals. They are not abundant and all those whose progeny have been observed were parthenogenetic.

The diffusion of the phylloxera is effected in nature by the wandering newly hatched larvæ of the radicicoles during summer and autumn. These pass from vine to vine, either on the surface of the soil or through subterranean cracks or pathways. They may also be borne by the wind or on vineyard material, such as picking boxes. Probably water is responsible for some diffusion in hilly or irrigated vineyards, and cultivating instruments by picking up pieces of infested roots may effect fresh infestations. The phylloxera is easily introduced into a vineyard or section by the practice of planting infested rooted vines to make up for cuttings which did not succeed in previous years.

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